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THE NASCENT FOREST OF THE MISCOU BEACH PLAIN.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 4.[1]

W. F. GANONG.

(WITH FOURTEEN FIGURES)

THE extreme northeastern angle of the Province of New Brunswick, as the accompanying map will show, is formed by the island of Miscou. The northwestern margin of this island is an extensive sandy beach plain, growing rapidly by action of the sea, locally called Grande Plaine. On this plain there is developing a forest which exhibits every stage of formation from the salt plants of the open sea beach to the heterogeneous vegetation of the mixed woods. The conditions are unusual and the phenomena of proportional interest. In August 1905 I was able to give the place some two weeks of observational study, with results which follow.

In all such studies as this the correct identification of the plants is of first importance, and identification is becoming a matter of such difficulty that only a professional systematist is competent authority. Accordingly I have sent all of my collections, including a specimen of every plant I found at Grande Plaine, to Professor M. L. FERNALD, of the Gray Herbarium of Harvard University, who has been so kind as to determine their identity, and, as well, to give me the names they should bear in accordance with the recommendations of the Vienna Congress. I wish here to express my indebtedness to him and my best thanks for this invaluable aid. Such is the origin of the nomenclature of this paper.

[1] No. 3 is in the BOT. GAZETTE **36**:161–186, 280–302, 349–367, 429–455. 1903.

As to previous literature of this particular subject, there is none. In 1886 Dr. G. U. HAY made a collection of Miscou plants for the Geological Survey of Canada, but no account of them was ever published, and no other botanist has heretofore been on the island. In many respects, however, as the reader will observe, the vegetation of this beach plain resembles closely the vegetation

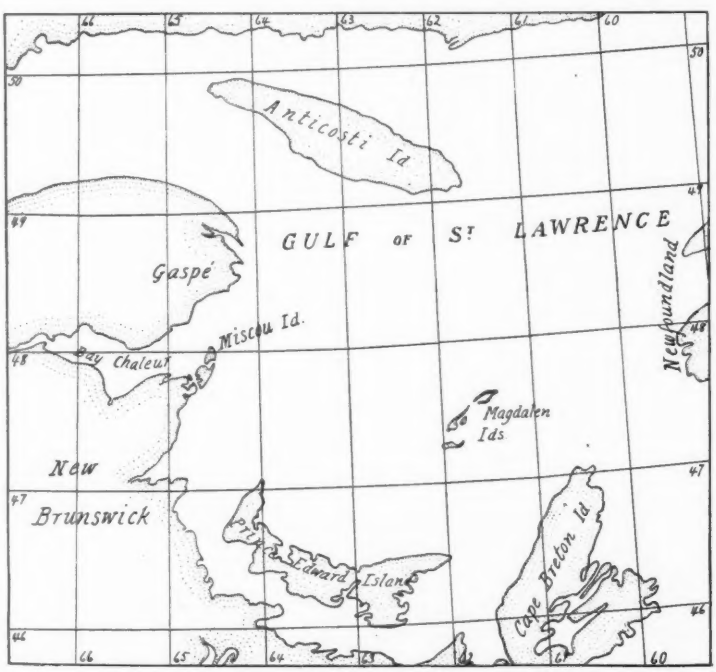


FIG. 1.—Outline map of part of the Gulf of St. Lawrence, to show the geographical position of Miscou Island.

of the sand beaches and dunes of Lake Michigan as described in COWLES'S well-known memoir,[2] and many of the conclusions of that work are also applicable here.

Grande Plaine extends along the west side of Miscou. Beginning on the south at Eel Brook (see the accompanying map, *fig. 2*),

[2] BOT. GAZETTE **27**:95–117, 167–202, 281–308, 361–391. 1899.

where it is but a few yards wide, it rapidly broadens northward until it reaches some half a mile across, and then narrows again towards its northern end, which is also the northernmost point of the island. Though nearly level as a whole, it is by no means flat, for it is composed of a series of approximately concentric dune beaches, which, two or three in number at Eel Brook, increase to over forty opposite Lac Frye. In height these dune beaches vary from two to five or six or even seven feet (0.6–2^{m}) and in breadth from eight or ten up to forty or fifty paces. At its widest part, which comprises some thirty or more of the beaches, new ones are plainly being rapidly added, while at its northern end the entire plain is being washed away by the sea, which is cutting sharply across the ends of the old beaches. About two-fifths of the plain, including the older parts next the upland, are forested; about two-fifths, including all the outer and newer parts, are open, clothed only by the waving beach grass; the intermediate zone, a small one-fifth of the area of the plain, is a

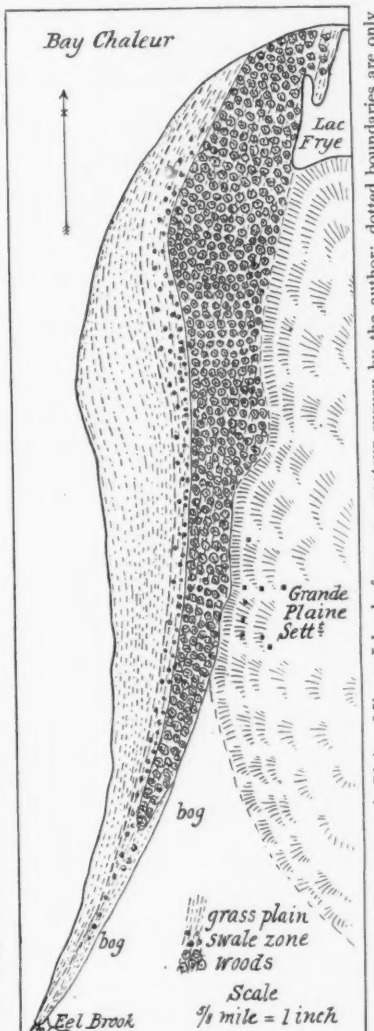


FIG. 2.—Map of Grande Plaine, Miscou Island; from an amateur survey by the author; dotted boundaries are only approximate; the heavier dotted line outside the swales represents approximately a line of higher dune beaches.

transition zone where the forest is pushing its advance into the open ground. The mode of formation of this remarkable plain, involving the anomaly of extensive land-building on a sinking coast, I have described somewhat fully elsewhere.[3] Briefly, the facts are these. As the result of peculiarities of the topography, wind, and tides of this region, there is formed on the shallow northwestern side of Miscou a kind of great eddy in which all movable materials, sand and gravel from the wear of the rapidly crumbling adjacent coasts, as well as driftwood, waterweeds, and other flotsam, often from a great distance, tend to collect, and thence are driven ashore by the prevailing westerly winds. Formerly the island extended farther north than now, carrying with it both eddy and plain; but the general subsidence actively in progress in this region has carried its low northerly end beneath the sea, thus forcing the eddy and the accompanying plain-building gradually southward. The northern end of Grande Plaine today is being rapidly washed away (compare map), to be redeposited farther south, and the plain as a whole is thus rolling by its outer margin southward along the coast. The subsidence of the land has produced another effect upon the plain, and one of considerable consequence to its vegetation, namely, its inner and older part averages somewhat lower, that is, less above sea-level, than the outer and newer part, thus leading to a settling of water towards the older inner parts, and a relatively higher water-table in them. That we have here a beach plain, instead of a series of lofty sand dunes, is the result of the fact, apparently, that the dry sand of the beach is blown ashore no faster than the beach grass can fix it. At both the northern and southern ends of the plain, however, there is some approach to a building of true, though low, dunes.

My brief study of the vegetation of Grande Plaine was entirely observational, not at all instrumental, nor do any meteorological or other exact physical data for this region exist. Grande Plaine lies at sea-level in latitude 48°, beside a shallow sea, warm in summer but frozen over in winter. The summer climate is remarkably equable, of a temperature most comfortable for man, with no fogs and but little cloudy weather. The rainfall must be not far from

[3] Bull. Nat. Hist. Soc. N. B. No. 24:453. 1906.

45 inches. Heavy winds from the west prevail in summer. The soil is of pure quartz sand derived from the wear of the gray carboniferous sandstones of the region, this sand having, of course, the usual relations to water-supply, mineral nutrients, etc. No other special factors with a bearing upon the vegetation appear to be prominent.

We turn now to consider the vegetation. Although it presents every gradation from humble herbs of the open beach to the densest woods, nevertheless the eye becomes accustomed to recognize, and the speech to designate, certain definite vegetational regions. These represent the modes or climaxes, as it were, in the vegetation curve —the parts which exhibit a distinctive character in the physiognomy of the whole. They are the following: (1) the new beach, (2) the grass plain, (3) the swales, (4) the sandy woods, (5) the closed woods.

THE NEW BEACH.

The characteristic open, or new, beach of Grande Plaine, the kind which best illustrates the mode of growth of the plain, is to be found opposite its middle and broadest part; for towards the northern and southern ends its structure is modified by local conditions of erosion and dune-building. Outside of all is a broad sloping inter-tidal beach of pure sand without vegetation (*fig. 3*). Above it is the narrow band between ordinary and extreme high tides, from which the drying sand is being driven landward by the winds; it is also vegetationless, or with but stragglers from the upper beach. Finally, there is that broad shelf, very well shown in the accompanying photograph (*fig. 4*), reached only by the very highest tides, composed of fine quartz sand, intermixed with some gravel and occasional flat cobbles; it is covered with scattered driftwood among and over which the dry sand is being forever driven, shifted, and piled. Thus the new beach offers a barren habitat to plants, for it has a mineral-poor soil, drenched often by salt, forever shifting, and exposed to the unbroken force of frequent heavy winds. The vegetation is plainly responsive to these conditions. It is extremely scanty, the plants growing widely isolated, while many square yards do not show any vegetation at all. Thus competition among the plants seems not to exist, and the struggle is wholly with the

physical environment. The most characteristic plant by far is the small, radiate-decumbent, succulent, annual saltwort, *Salsola*

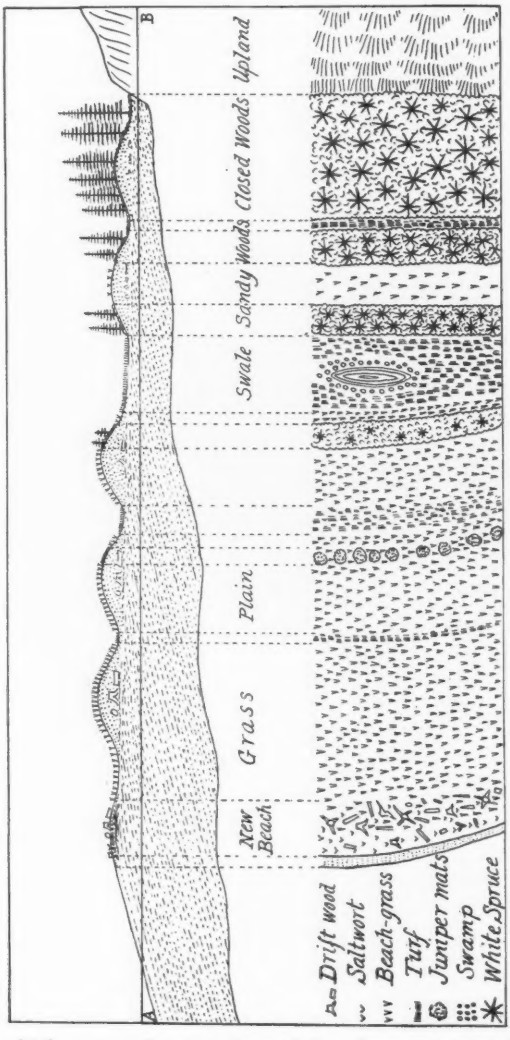


FIG. 3.—Idealized section and map to show the mode of formation of the beach plain, and the distribution of its vegetation; the line *AB* is true level, and may be taken to represent approximately the position of the water-table.

Kali, which occurs but rarely and for the most part in the lee of

some shelter, such as a hollow or large piece of driftwood. Next in abundance, though but scarce, is the little fleshy, rosette-like, annual sea rocket, *Cakile edentula* (*C. americana*). Third in abundance is the low halo-rosette, perennial sea lungwort, *Mertensia maritima*, here seemingly growing as an annual, also mostly in places of some shelter. Rarely, and then only in a sheltered position, occur tiny radiate-creeping plants of the beach pea, *Lathyrus maritimus*, growing apparently only as an annual, and sometimes showing a marked difference in the windward-creeping and leeward-

FIG. 4.—Typical open, or new, beach, looking north; among the driftwood occur scattered tufts of saltwort and beach grass.

creeping shoots on the same plant, the former being much shorter and smaller-leaved. Even rarer is the radiate-creeping, small-leaved, halo-scurfy annual, *Atriplex patula hastata*. Here and there, however, especially in sheltered places, arise the tufted culms of the beach grass, *Ammophila arenaria*, the characteristic sand-binding perennial of the dune beaches next to be considered, here seemingly growing from seed. I was able to find no other plants on the new beach. Thus we see that this vegetation is distinctly adjusted to the physical conditions, for it is of great paucity, of small and slow growth, annually renewed, closely ground-appressed, and strongly xerophytic.

THE GRASS PLAIN.

Inside the line of open beach begins the sand plain, composed of a great number of approximately parallel dune beaches, forming smoothly swelling ridges and hollows of elevations and breadths already described. Every dune beach, I believe, originates with a core of driftwood. As the tidal beach is built outwards by the addition of sand, driftwood continues to collect on its uppermost part, until finally some unusual combination of great winds with high tides sweeps it up beyond reach of further disturbance. Then the driving sand from the beach is caught among it; the beach grass gains a foothold in the sheltered places, spreads, and checks the further movement of this sand. Then more sand is driven shoreward, and it grows into a low dune which is fixed by the beach grass as fast as it rises. The limit is reached only when a new line of driftwood has been formed outside and begins to stop the sand for its own growth. The resultant dune beach offers severe conditions for plant life, for its surface is swept, especially on the summit and windward slope, by heavy winds; it is heated intensely by the sun; it is readily movable; and it forms a soil extremely poor in mineral nutrients.[4] It lacks the salt of the newer beaches, however, for this is soon removed by the rain; and it possesses an ample supply of moisture a foot or two beneath the surface, for the supply brought by the rain drains but slowly away, owing to the low gradient of the water-table. These conditions, especially at their extreme on the summits and windward slopes of the beach dunes, are endured by practically but a single plant—the herbaceous-perennial, subterranean-creeping, xero-culmed, deep-rooting beach grass, *Ammophila arenaria*, which occurs, without any competitor whatever, in open scattered tussocks, only partially covering the ground, as well shown in *fig. 5*, and in closer view in *figs. 6* and *7*. It happens that this grass is of considerable economic value to the neighboring farmers, who cut it and haul it for hay, and whose cattle graze upon it; its destruction in this way causes an irregular exposure of the outer beaches, permitting them to be irregularly cut by the wind. It is for this reason, I have no doubt, the newer outer beaches

[4] As indicated by KEARNEY'S recent studies: BOT. GAZETTE **37**:426–436. 1904.

are so much more irregular in their various characters than the older inner beaches, which antedate the advent of man.

But while the beach grass has no competitor, it affords a shelter, especially behind its tussocks, permitting the growth of a number of other plants, which, however, form but an insignificant part of the entire vegetation, and which are widely separated from one another. Most important of these, perhaps, is the beach sedge *Carex silicea*, which grows in scattered tussocks here and there among the beach grass, and it is indeed the only other plant which

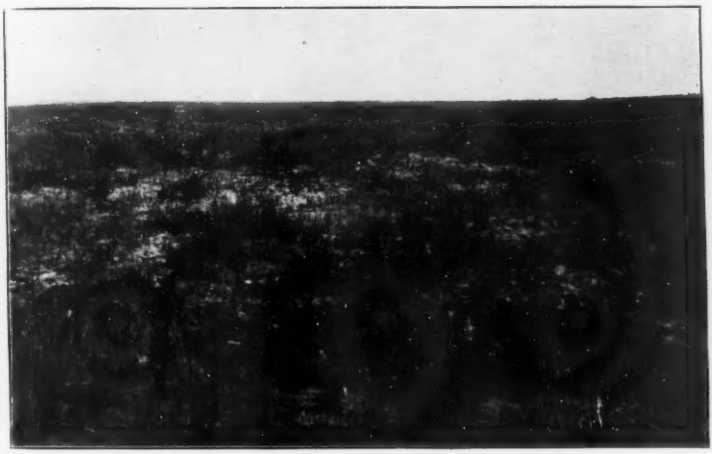


FIG. 5.—Typical grass plain, looking north; practically no plant visible except the beach grass.

seems at home in this situation. The remainder of the plants, all sparsely or rarely represented, are obviously stragglers from the most diverse habitats, many of them quite unexpected residents in such a situation. Thus, dwarfed saltwort strays in from the beach, and the beach pea is here somewhat more flourishing than on the open beach. Then there are greatly dwarfed individuals of certain ubiquitous forms able to endure a wide range of physical conditions, such as the dandelion, *Taraxacum officinale*, which extends in sheltered spots even to the outer margin of the plain; the Canada thistle, *Cnicus arvensis;* the sow thistle, *Sonchus arvensis;* the

field sorrel, *Rumex Acetosella*, in dwarfed-rosette, very red forms; the evening primrose, *Oenothera biennis;* and the moonwort, *Botrychium ternatum intermedium*. There are also some forms usually characteristic of rather a dry habitat, such as the pearly everlasting, *Anaphalis margaritacea*, and a western yarrow, *Achillea lanulosa*. In addition there are others, generally in more sheltered spots and also greatly dwarfed, which usually prefer a moister habitat, such as the two western roses, *Rosa acicularis* (*R. Sayi*, *R. Engelmanni*) and *Rosa lucida;* a western violet, *Viola adunca;* a stitchwort, *Stellaria longipes laeta;* a silver weed, *Potentilla Anserina concolor;* the stellate false Solomon's seal, *Smilacina stellata;* and one of the vetches, *Vicia Cracca*.[5] The great diversity of natural habit of these plants, their scanty and irregular occurrence, and their dwarfed size and rosette-forming tendency all unite to show that none of them are here at home. Obviously they are the ones which, of all the many kinds which must be brought to this plain by natural modes of dissemination, are sufficiently tolerant physiologically to be able to germinate under, and then to withstand, these extreme physical conditions, eking out here a starved and precarious existence. The conditions for germination upon the sand must be extremely severe, and it is very likely that other kinds of plants could exist here as adults, could their seeds develop; and further it is probable that the individuals which do exist on the plain are those whose seeds happened to fall in especially favorable spots, or became properly buried by the moving sand. Else why are they so few? The universal dwarfing is due in all likelihood not to the heat and dryness of the surface, nor to any salt content in the soil, and certainly not to a scarcity of soil water, but to the paucity of mineral nutrients in the sand. This is in harmony with another feature they mostly show in common—very deep and, I think, much-branching roots. The fact that they come

[5] The following Grande Plaine plants appear to be new to the flora of New Brunswick: *Achillea lanulosa*, *Viola adunca*, *Rosa acicularis*, *Stellaria longipes laeta*, and *Potentilla Anserina concolor*. Certain others are new in name, the species having been recently more exactly defined and segregated: *Alnus mollis*, *Myrica carolinensis*, *Vaccinium Vitis-Idaea minor*. Others are new in name because made to conform to the rules of the Vienna Congress, but in these cases the names of Gray's *Manual*, 6th edition, have been given in brackets.

from such a diversity of natural habitats, and yet live in this peculiar situation upon an equal footing, shows how far we are from understanding the real bases of physiological adaptation, and further shows that in the study of the physiological life-histories of plants lies the most important and attractive field for the ecologist of the near future.

So much for the exposed parts of the dune beaches. But in addition they offer, upon their inner or leeward slopes and in the hollows, situations more sheltered, not so much from the sun, since

FIG. 6.—Typical hollow between outer dune beaches; the tall grass is all beach grass, but the small plants among it are the common strawberry.

their average course is nearly north and south, but from the westerly winds. The older inner dune beaches also are protected to some extent by the newer outer ones, as well as by their slightly lower average level. The difference between leeward slope and hollow is not simply one of degree of shelter, however, but also of physical conditions, for the hollow is much nearer the source of water supply, the free table of which is not over a foot or two beneath the surface. In consequence of these differences we can recognize three distinct phases of vegetation: *first*, a larger development on the leeward

slopes of plants which are small and rare on the outer slopes; *second*, a distinctive vegetation of the hollows; and, *third*, a distinctive vegetation of the inner slopes.

As to the first phase, it is enough to note that several plants, in particular the pearly everlasting and the wild roses, small, scarce, and scattered on the outer slopes, become larger, frequent, and even patch-forming on the inner; and this is true also in less degree of other species. The beach grass persists in all situations.

The second phase is the vegetation of the hollows. The very first plant to appear in this situation, and that too near the outer beaches, is always, strangely enough, the common wild strawberry, *Fragaria virginiana*, apparently of normal size and form, seemingly quite at home, and spreading abundantly by runners, so that it forms considerable patches. The appearance of the nascent patches is well shown in *fig. 6*. As soon as the patches reach an appreciable density, such that they afford a cover to the ground, then turf-forming grasses, of which the first is the red fescue, *Festuca rubra*, appear and initiate the turf-formation which is so important a feature of the swales to be described below. The strawberry, of course, is one of the most tolerant, and hence ubiquitous, herbs of our flora, and its situation here is partially explained by the nearness of the abundant water supply. Yet it is surprising to find it taking so important a part in a vegetation in so peculiar a position.

The third phase of this vegetation is that characteristic of the sheltered slopes. First of such plants to appear, and the most common and characteristic, is the dwarf creeping juniper, *Juniperus Sabina procumbens*, of which single plants originate just below the beach dune crests, and creep radiating, more to leeward than to windward, in a close dense mat covering many square feet. A young plant is shown in *fig. 7*, in characteristic form and position. On the inner beaches these plants occur upon the outer as well as the inner slopes, and the shelter of the mats thus formed affords in reality the principal starting-point for the development of other plants which lead gradually to the development of the forest, as will be noted under the transition vegetation. In a similar situation, but independently, arise patches of two other characteristic plants, a bright-green, leathery-leaved, tufted shrub, the wax berry,

Myrica carolinensis, which comes to form dense discoid (sometimes almost fairy-ring like) masses on the crests and inner slopes; and the less frequent, low, dense-tufted, white-hairy shrub, *Hudsonia tomentosa*, in irregular close patches. All of these plants are pronounced xerophytes, which amply explains their ability to live in this situation, and even their preference for the somewhat drier upper slopes of the dune beaches. Their xerophilism, in common with that of many other evergreen sand plants, is, as I guess it, an

FIG. 7.—Typical upper inner slope of a dune beach; the grass is beach grass, but in the center is a typical plant of dwarf creeping juniper.

adaptation to the physiological dryness which results when, as must often be the case in spring and fall, the ground water is of low temperature and hence slowly absorbed, while the leaves are exposed to high transpiration conditions from the bright sun, heat reflected from the sand, and high winds.[6] The juniper, while perfectly at home here, apparently is so only through coincidence, for its original habitat is seemingly dry rocky hills. But the other

[6] This principle, which from its discoverers we may call the KIHLMAN-GOEBEL principle, seems to me deserving of much more recognition than our students are inclined to give it. At least it calls for careful experimental investigation.

two, the waxberry and the Hudsonia, are characteristic of just this situation, in and to which they have apparently been adaptively developed. Towards the inner dune beaches another low shrub comes in on the slopes, though dwarfed and not abundant, the common blueberry, *Vaccinium pennsylvanicum;* it is evidently not here at home, but its somewhat xerophytic habit permits it to exist. As these various plants grow older and extend their patches, they run together more or less, sometimes two, sometimes three, and even all four. Later others are added to them, initiating the juniper mats and the woods carpet, later to be considered.

The contrast between the vegetation of the outer and the sheltered slopes of the dune beaches comes out with striking clearness a few hundred yards north of Eel Brook, where it happens the entire plain is very narrow, and slopes in both directions from a central higher crest. Outside of this can be seen only the beach grass and its accompanying forms as listed above, while inside the various xerophytic shrubs show to great perfection.

THE SWALES.

Between the open grass plain and the woods occurs a transition zone marked not only by an intermediate vegetation but also by distinctive physical features as well. First of all it is characterized by the presence of several great turf-carpeted and tree-bordered swales, morphologically hollows between the dune beaches which here spread much farther apart than usual. They are well shown in *figs. 8, 10, 11.* They are best developed in the widest part of the plain, hardly occurring towards its southern or northern ends, and outside of them runs a line of higher dune beaches, which indeed can be traced through most or all the length of the plain (*fig. 2*). The swales are narrow southward, but broaden northward, deepening as they go, until in some cases they dip beneath the water-table (thus exhibiting pools), after which they rapidly narrow and rise to disappear northward. Again, the trees of this zone, occurring always along the slopes of the dune beaches, do not exhibit a transition of size and age to those of the sandy woods, but are always so much smaller and younger as to be sharply marked off from them, the case shown in *fig. 10* being very exceptional, and that of *fig. 8*

more typical. Again, the transition from the broad swales to the beaches of the sandy woods is most abrupt, for the latter are regular, narrow, close together with scarcely any hollows between, and also exhibit a curious barrenness on their summits in marked contrast to the better-clothed summits farther out (compare *figs. 8* and *13*). Unfortunately the full importance of these features did not strike me in time for a study of them on the ground, but such data as I possess in notes and maps lead me to believe that the swales are much newer in origin than the beaches immediately inside them, and that they mark the transition from an older series of beaches which formed part of the original Grande Plaine extending far to

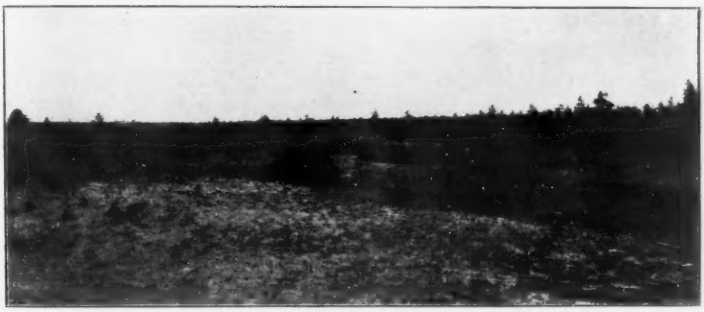


FIG. 8.—Typical transition zone, looking north; showing a swale on the right, with its sharp line of transition to the woods; the trees are all white spruce.

the north of the present island, and a newer series formed by the rolling of the plain down the coast, as described earlier in this paper. All the facts I possess both as to geography and vegetation are consistent with this view.[7]

Aside from the question of age, the swale zone differs physically from the grass plain by its greater shelter from the west winds, its lower level and greater nearness to the water-table, a probable increase of mineral nutrients derived from decaying driftwood and diffusion from the upland, and some slight accumulation of humus.

[7] And it is sustained by the tradition of the residents who say that the plain has been built out from the edge of the woods almost within the memory of men still living. I have discussed the subject more fully in Bull. Nat. Hist. Soc. N. B. No. 24:456. 1906.

The vegetation consists broadly of a higher development of the vegetation of the inner grass plain—the scanty turf of the hollows becoming the broad expanse of meadow turf of the swales, and the juniper mats extending greatly with the addition of many young white spruces. So distinct are the turf of the swales and the juniper mats, with their trees, from one another, that there result glades and vistas of park-like and charming aspect, as shown especially well in *fig. 8*.

First in importance are the juniper mats, for they inaugurate the woods. These mats, composed either of large radiating patches of this plant, or else variously united and combined with patches of waxberry, Hudsonia, and blueberry, extend greatly in diameter, covering the crests as well as the slopes of the dune beaches, and thus form a woody net in the shelter of which several other forms, mostly markedly dwarfed, gain foothold. A typical example is shown in *fig. 9*. Some of the plants of the grass plain persist, especially the beach grass, pearly everlasting, and yarrow. The new forms which appear are, first of all, the common crowberry, *Empetrum nigrum*, and the rock cranberry, *Vaccinium Vitis-Idaea minor*, followed closely by the three-toothed cinquefoil, *Potentilla tridentata*, all of them plants characteristic of dry upland rocky situations. Less frequent are the little gentian, *Gentiana Amarella acuta*, and the large cranberry, *Vaccinium macrocarpon*, plants belonging to moist places. And when the mats are especially well developed there come in, as shown in *fig. 9*, the reindeer lichen, *Cladonia rangiferа*, and a brown moss which I take to be the *Aulacomnium palustre* (so much more highly developed in the woods), another curious mixture of xerophytic and hydrophytic forms. We have therefore upon these juniper mats a very heterogeneous assemblage of forms drawn from diverse natural habitats all the way from rocky hills to bogs. They do not exist here, therefore, in virtue of adaptation to this position, but plainly represent those forms of the flora of this region whose adaptations happen to fit these conditions, or whose range of physiological toleration happens to be great enough to permit endurance of the conditions here. Of these matters we shall know more in the future, but their mention helps to emphasize how large an element of accident or incident

there is in adaptation, and how likely it is that adaptation will ultimately prove to be a matter of the loose and large rather than of the exact and minute.

Finally, it is in this same situation, upon the upper slopes of the dune beaches, and usually, but not always, on the juniper mats, that the characteristic trees of the zone, the white spruce, *Picea alba*, develop. Standing in open formation, they do not interfere with one another's growth, and in consequence become,

FIG. 9.—Typical large juniper mat on a slope and crest of a dune beach, with a number of associated plants noted in the text; looking south.

except for wind effects, symmetrical in outline and clothed to the ground. They occupy that situation no doubt for the same reason that the shrubs do, as a compromise between the greater wetness of the hollows and the greater dryness of the beach summits. This habit of growing thus upon the slopes, and not on summits or hollows, has a most important effect upon the physiognomy of the vegetation in this zone; for to it is due the openness of the swales, with their regular borders of trees, and as well the openness of the beach summits in the sandy woods later to be noticed. Toward the sea the spruces are small and dense, and often show, as in *fig. 11*,

pronounced wind effects. In places many seedling trees may be found, though the distribution of these is curiously irregular. In one place only did I find any other tree, and that was a single specimen of the prince's pine, *Pinus Banksiana*.

If it be asked why the white spruce is the first tree to develop on these plains instead of some other of those growing on the upland near by, I can only say that an answer must wait until we know something about the physiology of the white spruce and of other trees of the vicinity.

We turn next to the swales, those long open hollows carpeted by a close turf, and bordered by spruces. The general appearance

FIG. 10.—Highly developed swale, looking south; on the left is the edge of the sandy woods with old trees, and on the right a line of much younger trees, here much larger than usual.

of the turf is well shown on the right in *fig. 8*, and extremely well in *fig. 10*, which shows perhaps the best-developed of all the swales. The turf is a good deal modified in vegetation by the grazing of cattle and horses, yet its general characters show plainly enough. Originating in the outer hollows with the strawberry, as already noted, the real turf begins with the red fescue grass, *Festuca rubra* (*F. ovina rubra*), which soon drives out the strawberry. To this, as it becomes compact in the inner hollows, other grasses are rapidly added, especially the June grass, *Poa pratensis*, and then the brown top, *Agrostis alba*. After these comes a rush, *Juncus Vaseyi*, and the little sedge, *Carex Oederi*. Very likely, also, there are other

grasses which, owing to my imperfect knowledge of those groups, I overlooked. On and among these plants occur others, among which I have collected the following: the eyebright, *Euphrasia americana* (*E. officinalis*); the bugle weed, *Lycopus uniflorus* (*L. virginianus*); a tiny everlasting, *Antennaria neodioica;* a pearlwort, *Sagina procumbens;* the plantain, *Plantago major;* the two common cinquefoils, *Potentilla norvegica* and *Anserina;* the fall dandelion, *Leontodon autumnale;* and the white clover, *Trifolium repens.* These forms, in common with the grasses, are all greatly dwarfed

FIG. 11.—An outer swale, looking north; in the center clumps of blue flag; on the slope on the left white spruce and waxberry; on the right is a low depression with a thicket of poplar (the white spruce among it being on a local elevation).

and derived from diverse habitats, and are evidently a collection of heterogeneous stragglers from the neighborhood, held together by no stronger bond than ability to eke out existence in this inhospitable position. The majority belong to somewhat moist places, and they find an ample supply of water; for the water-table even in the driest summer is within a foot of the surface, and of the sweetest water. Evidently it is not dryness which stunts the forms, but most likely, as I believe, paucity of mineral nutrients. The turf represents the first closed formation we have met with, and

competition may therefore determine some of its minor features, but to these I gave no attention.

The turf reaches its climax in the open swales like those shown by *fig. 10*. In the woods it disappears, as will be noted under the next section; but towards the lower levels, especially towards the pools of standing water, it gives way gradually, by definite steps, to an assemblage of true swamp plants. The very first of these to appear in the lower places in the swales is always the common blue flag, *Iris versicolor*, and characteristic scattered clumps of this plant may be seen in the foreground in *fig. 11*, in the distance

FIG. 12.—Marshy swale, looking south; in the center a permanent pool with margin trodden by cattle; behind it are cat-tails and rushes, and back of them a thicket of poplar; on both right and left is sweet gale, and in the foreground is the blue flag.

on the swale in *fig. 8*, and on the left margin of the swale in *fig. 10*. Next follows always the sweet gale, *Myrica Gale*, and after that low bushes of the balsam poplar, *Populus balsamifera*, a plant which forms very dense thickets and grows larger as the situation is more sheltered. Finally the pools of standing water are reached, and on their margin occur cat-tails, rushes, and mare's tail, *Hippuris vulgaris*, with some other forms which I have not attempted especially to study. The plants may be variously combined according to local circumstances, but a very typical arrangement is shown in *fig. 12*. It is plain that we are dealing here simply with an ordinary

swamp, offering nothing peculiar unless it be the small size of some of the plants, notably the poplar. But these places develop yet farther in time, and there come in after the poplar three willows: *Salix balsamifera*, *S. lucida*, and *S. candida*, forming very dense thickets, and apparently under congenial conditions. Finally comes in the alder, which appears to be mostly a form of the green alder, *Alnus mollis*, giving us the culmination of the swale thickets.

THE SANDY WOODS.

Inside the swale zone, through almost the whole length of the plain, extends a narrow zone, only some four or five dune beaches

FIG. 13.—Typical sandy woods, just inside the swales, looking north; in the center a dune beach, bearing scanty beach grass and reindeer lichen, while on the slopes are small juniper mats with white spruces.

wide, of remarkable sandy woods, whose characters are well shown by *fig. 13*. Their most striking feature is perhaps the relative bareness of the tops of the beaches, which remain far more clear of vegetation than do most of the beaches outside of them; and this bareness, in conjunction with the presence of trees on the slopes and in the hollows, gives rise to curious vistas as shown by the photograph. The bareness must have some physical basis, but I was not able to discover it. These dune beaches, further, are very narrow, low, and regular, with hardly any true hollows between, so that the turf

from the swales is very scanty, almost wanting, in this zone. Further, the trees, all of them white spruces, are much older than those of the swale zone, the transition being commonly of the most marked abruptness. All of these features tend to emphasize the conclusion earlier given, that there is an abrupt physical difference between the beaches of these woods and those outside, a difference which, I feel sure, is one of age. The position of the zone would indicate that it possesses more favorable physical conditions as to water, mineral supply, and shelter than the zone outside, with which the large size of the trees is in agreement. But the bigness of the trees makes the barrenness of the beaches all the harder to explain. In their vegetation the sandy woods exhibit three divisions: the sparse, scattered beach grass and reindeer lichen (*fig. 13*) on the beach crests already mentioned; a few and small patches of turf which can hardly obtain a foothold where the hollows are so small; and the juniper mats in the slopes and hollows with their well-grown white spruces. The mats, however, are no longer entirely creeping, for the junipers send up numerous erect shoots. With them persist several of the plants from the transition zone, especially the rock cranberry, the three-toothed cinquefoil, the pearly everlasting, and a few others. But in addition new forms come in, especially and characteristically the bearberry, *Arctostaphylos Uva-ursi*, a rocky-hill plant, here creeping radiately over the sand, apparently under congenial conditions. Beneath the shelter of the trees appear some plants of the woods carpet which we may best consider under the next section. The trees themselves are of moderate size, rarely if ever over 20 feet in height.

A fact of interest about the juniper mats, applying also to a less degree to the forest mat which succeeds it in the closed woods, is its very slight hold upon existence on the sand, for where teams cross and disturb it, the entire mat dies and soon disappears. Such instability shows forcibly how hard are the conditions of life in this situation, and how narrow the margin between success and failure.

THE CLOSED WOODS.

The climax of the sand-plain vegetation is reached in the dense though dwarfed mixed woods extending between the sandy woods and the upland. A typical view of the closed woods is shown by *fig. 14*.

Physically the situation is much more protected than the zones outside of it, and, lying at a still lower level, it has a moister soil. The soil, however, is still of sand, though it contains some humus from the decaying vegetation and must derive some mineral matter by diffusion and drainage from the upland. Very likely also the sand is shallower here than farther out (*fig. 2*), and hence some influence of the minerals of the underlying soil may be felt, while in places an appreciable enriching of the soil must result from the decay of

FIG. 14.—Typical closed woods, chiefly of white spruce, but with some deciduous trees in the background; the closed forest carpet shows in the glade of the left foreground.

the bodies of the walrus, formerly slain here in great numbers, as manifest by their semi-fossil bones.[8] These additional sources of mineral nutrients, however, by no means furnish a supply sufficient for the proper growth of the woods, for in every feature they exhibit marked depauperation as compared with the same species on the neighboring upland.

In relation to the preceding zone, the closed woods consist essen-

[8] Described more fully in a note in Bull. Nat. Hist. Soc. N. B. No. 24:462. 1906.

tially of a greater development of the juniper mats, which unite to form a complete unbroken carpet, together with a greater development, both in number and size, of the white spruce trees, to which are added some deciduous trees and shrubs. And where the hollows dip lower than usual, and towards the upland in places, this forest merges to alder and cedar swamp.

We consider first the woods carpet. Morphologically it is a direct development of the juniper mats of the outer zones, though but little juniper, aside from occasional erect shoots, is left. With it persist some of its earlier associates, the rock cranberry, three-leaved cinquefoil, some grasses, the bearberry, and the reindeer lichen, varying in their respective development according to situation. To these are now added dwarf plants of the bunchberry, *Cornus canadensis*, the twin flower, *Linnaea borealis americana*, *Pyrola chlorantha*, the pipsissewa, *Chimaphila umbellata*, and an abundant brown moss, which has been identified for me by Mr. A. J. GROUT as *Aulacomnium palustre*, a typical swamp moss. Upon this carpet develop a few larger forms, especially the abundant wild sarsaparilla, *Aralia nudicaulis*, the gooseberry, *Ribes oxyacanthoides*, the dwarf raspberry, *Rubus triflorus*, with others less conspicuous.

We consider next the trees of these woods. First in importance and size, far surpassing all others in both respects, is the white spruce. It attains a height of perhaps 7.5^{m}, a diameter near the ground of perhaps 45^{cm}, and it exhibits over 100 annual rings, though perhaps some may be much older than those I counted, which were cut by the residents for wood. The next to appear is the balsam fir, *Abies balsamea*, becoming somewhat abundant and characterized by a spruce-like arrangement of its leaves all around the stems. Then follow the red maple, *Acer rubrum*, the aspen, *Populus tremuloides*, the paper birch, *Betula alba papyrifera* (in very small trees however), and the mountain ash, *Pyrus americana;* while the common undershrubs are the red dogwood, *Cornus stolonifera*, and the black alder, *Ilex verticillata*. There are probably some others, but these I believe are all that are notable.

In especially low places, such as in certain hollows, and at the contact of plain and upland, the conditions verge towards those of

a swamp, and swamp plants appear—the iris, the sweet gale, some mints, species of Galium, and the dewberry; while the spruce gives way to the white cedar, *Thuja occidentalis*, and the alder becomes abundant, forming a dense jungle. But this is of less interest than the vegetation of the outer zones, and hence I gave it little study.

Thus it appears that these woods present no features, size of the plants alone excepted, markedly different from those of woods preponderatingly coniferous in the neighboring upland, and they are evidently tending towards the typical woods of this region—the mixed coniferous-deciduous forest.

We have thus another illustration of that principle so important in physiognomic ecology, that vegetation, no matter under what immediate physical conditions it may be, is always tending towards a climax type, determined primarily by climate.

CONCLUSION.

In this paper I have tried to state the facts about the vegetation of a somewhat remarkable place, adding thereto some ecological comment whose chief value is to illustrate our ignorance of that subject. As I understand it, such descriptions as this aims to be may have three values. First, they can present to all who have interest in such matters a series of pictures, as vivid and realistic as possible, of the vegetation of special places, and they are the more valuable according as they are the more clearly and attractively written and the more aptly illustrated. Second, they should help to supply information, badly needed by all of our manuals, about the natural habitats of the common or important species of plants. Third, they can form storehouses of facts about vegetation upon which the future student can draw as the advance of physiological ecology gradually makes possible an understanding of the principles underlying physiognomic ecology. Such descriptive work can be done to profit by the student whose work is perforce confined to his summer vacations, if he but bring to it time and care enough; but he should be content to describe well and to leave interpretation to the field physiologist yet to come. Speculation cannot of itself advance knowledge, and it can bring a subject into disrepute. It is only, I believe, through field physiology, the study

in field laboratories of fundamental plant-dynamics, that ecological knowledge can really be advanced. And the dynamical problems, as I see them, fall under these heads, in the order of importance: (*a*) physiological life-histories of species, (*b*) physics and chemistry of the soil, (*c*) nature of plant-competition, (*d*) a better correlation of meteorological data with physiological phenomena.

SMITH COLLEGE,
Northampton, Mass.

THE DEVELOPMENT AND ANATOMY OF SARRACENIA PURPUREA.[1]

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY. No. 5.

FORREST SHREVE.

(WITH PLATES III–V)

THE work of which the results are here given was undertaken at the suggestion of Dr. D. S. JOHNSON, and has been carried out at the Biological Laboratory of the Johns Hopkins University. I wish here to express my thanks to Dr. JOHNSON for much advice and helpful criticism in connection with this work, and to express to Professor WILLIAM K. BROOKS my appreciation of his interest and encouragement. I also wish to thank my fellow-student Mr. SAMUEL RITTENHOUSE for his kindness in gathering material for me during my absence from Baltimore.

The material worked upon was obtained mainly at Glenburnie, Maryland, near Baltimore. Most of it was fixed in the field; and of several killing reagents tried 1 per cent. chrom-acetic and Carnoy's mixture were the most satisfactory. Preparations mere made by ordinary paraffin method and stained with the Flemming triple stain or with cyanin and erythrosin.

DEVELOPMENT OF THE FLOWER.

The earliest stage observed in the development of the flower was in material gathered August 30. There are then to be seen the primordia of the three bracts, the five sepals, and the five petals, which have apparently arisen in the order named. Lying just within the edges of the petals are the staminal primordia, as yet mere papillae, and within them is a flat surface with slight elevation at the center. A somewhat later stage than the last shows progress in the development of the stamens, which now appear as ten groups of protuberances lying in the position before noted (*fig. 2*). Each

[1] Dissertation submitted to the Board of University Studies of the Johns Hopkins University for the degree of Doctor of Philosophy.

group arises from a base which is distinct from the bases of the adjoining groups, and is made up of the primordia of five to eight stamens. There is no suggestion of a pairing of the groups nor of their falling in two whorls. Upon the central flat surface has arisen the ovary, which at its base is pentagonal in outline, and at its apex is surmounted at the angles of the pentagon by the tips of the carpellary leaves. The outgrowths of the wall of the ovary which are destined to give rise to the placentae are upon the sides of the pentagon, which shows each placenta to be made up of the edges of two carpellary leaves (*figs. 2, 14*).

MICROSPORANGIUM AND MICROSPORE.

The staminal primordia early show differentiation into parts destined to give rise to filament and anther. The latter portion bears approximately the same outline in cross section as do the mature anthers. The location of the archesporium is indicated at first only by the slightly greater size of the nuclei in the region of the four microsporangia (*fig. 4*), but soon comes to be more sharply defined by the concentric arrangement of cells in the region of the future parietal cells. The archesporium is at this earliest recognizable stage about six cells in cross section, but grows rapidly to about twelve cells in diameter (*fig. 5*). Development proceeds in the autumn to the differentiation of the endothecium, the two or three parietal layers, and the pollen mother cells. There is yet no distinction of definitive sporogenous cells and tapetum. In this condition the stamens pass the winter.

The elongated parietal cells do not contribute to the tapetum, but it is made up entirely from the isodiametric cells of the archesporium. The outer outline of the tapetal layer is continuous, and the inner is irregular only to an extent which makes it in some places two cells in thickness and in other places three. The cells of the tapetum do not wander among the definitive sporogenous cells Shortly after the differentiation of the tapetum, and before the pollen mother cells are in the synapsis stage, the tapetal nuclei divide once by mitosis, and so far as observed once only. At the time of tetrad division the tapetal nuclei are enlarged, the chromatin is granular and scattered, and the nucleoli are large. At the time of the forma-

tion of the walls of the pollen grain the cytoplasm of the tapetal cells becomes much vacuolated and the nuclei lose their chromatin; but at no time does the layer become broken. The parietal layers at the time of the tetrad division are three to five in number, the endothecium is thickened on its inner and lateral walls, and the epidermis is undifferentiated. The thickening of the endothecium walls takes places very late—simultaneously with the division of the pollen grain nucleus—the cells for some time previous to this being filled with starch.

Dehiscence is by means of two longitudinal slits, each of which opens two pollen sacs of the anther. A deep crease runs between each pair of pollen sacs upon the two sides of the anther, penetrating to the point at which the two microsporangia lie nearest each other (*fig. 13*). At this point is a group of small cells reaching from one microsporangium to the other, the walls of which are thrown into creases and folds, and fail to thicken in the further development of the anther, as do the neighboring cells.

The pollen mother cells apparently lie in the synapsis stage for several days. At their first division it is possible to count the chromosomes, the reduced number being twelve and their form short and blunt (*fig. 8*).

The tetrad division is simultaneous, there being no formation of wall after the first division. After a short period of adherence in tetrads the pollen grains round off and acquire the coats. The mature pollen grain is marked with eight meridional grooves so as to resemble a muskmelon. Beneath the grooves the intine is several times thicker than between the grooves (*fig. 11*). While the pollen grain is yet within the anther the nuclear division takes place which gives rise to tube and generative nuclei (*fig. 12*). In this condition the grains are shed, the stamens nearest the ovary opening first, and the outer ones successively.

OVULE AND MEGASPORE.

The placental outgrowths which arise from the flat sides of the ovary, at the point of juncture of the edges of the carpellary leaves, grow inward almost to the center of the ovary, and these I shall designate as the "main placental outgrowths" (*fig. 14*). Each

main placental outgrowth sends out two lateral outgrowths so as to resemble in cross section a letter T, in which the arms have been bent downward. Each pair of adjoining lateral outgrowths is closely appressed and directed backward toward the angles of the ovary. In the lower part of the ovary the adjacent lateral outgrowths fuse, but do not extend to the bottom, and in the upper part they do not reach the wall of the ovary as do the main placental outgrowths. Upon the edges of the lateral outgrowths and upon the surfaces lying next the main outgrowths are borne the ovules (*fig. 15*). The ovules at the base and top of the ovary lie parallel to the axis of the flower, those in the middle lie at right angles to it, the intermediate ones having intermediate positions according to their place in the ovary.

The summits of the carpellary leaves broaden and coalesce, and grow out in a direction radial to the axis of the flower, so that while their basal parts form the capsule and the stalk of the style, the tips form the umbrella of the style (*fig. 3*). The tip of each carpellary leaf organizes a very definite growing-point (*fig. 28*), and the portion between the tips nearly keeps pace in growth. Upon the ventral surface of each tip, just before it completes its growth, is formed the protuberance which bears the stigmatic surface.

The appearance of the primordia of the ovules upon the placentae takes place from the point opposite the angle of the ovary wall, where the adajcent lateral outgrowths meet, successively toward the angle formed by the lateral outgrowth and the main outgrowth (*fig. 19*). In vertical direction the development proceeds from the middle of the placenta toward top and bottom. The ovules first appear as protuberances initiated by the periclinal division of subepidermal cells and the accompanying anticlinal division of the epidermal cells, as is commonly the case. When the ovule first protrudes from the placenta there is no suggestion of a sporogenous cell. At this stage of development the winter rest intervenes. The first suggestion of a sporogenous cell comes with the enlargement of a single subepidermal cell, which is the megaspore mother cell (*fig. 16*). In three cases out of many hundreds examined there were two mother cells lying side by side. There is no tapetal cell. The bending by which the ovule becomes anatropous begins at once, and is quite

marked by the time of the appearance of the mother cell. Both transverse and longitudinal sections (*figs. 16* and *17*) show a double layer of cells at the sides of the mother cell, and median longitudinal sections show approximately five rows of cells in the ovule, exclusive of the epidermis.

The integument is single, its development beginning by periclinal divisions of subepidermal cells upon the convex side of the bending ovule, and continuing as a ring which grows rapidly on the side where it began first and slowly on the opposite side, which lies next the raphe. The rapid growth of the ovule is accomplished largely by the chalazal end. By the time of the first division of the mother cell the bending of the ovule is completed, the integument has grown so as nearly to close the micropyle, and the mother cell has increased in size and encroached upon the nucellar tissue so as to lie next the epidermal cells over the entire distal end (*fig. 20*).

The difference in the time of appearance of the ovules upon the different parts of the placenta causes a difference in the degree to which the integuments develop (*fig. 19*), and also a difference in the maturation of the mother cell, and the germination of the megaspore in ovules in the different parts of the placenta, a difference which long remains evident.

At the first division of the mother cell it was not found possible to count the number of chromosomes. The division is followed by the formation of a wall (*fig. 20*), and in about half the cases observed both the daughter cells again divide to form the normal linear tetrad of megaspores (*fig. 23*). In the remaining cases the micropylar daughter cell fails to divide, resulting in a series of three megaspores (*fig. 21*); and much less frequently the micropylar daughter cell divides by a wall parallel or nearly parallel to the long axis of the nucellus (*fig. 22*). In any case it is the chalazal megaspore which functions, the micropylar ones being appressed to the layer of nucellus and absorbed. The maturation of the megaspore is coincident with the tetrad division of the microspore mother cells.

EMBRYO SAC.

Such has been the elongation of the ovule by the time the megaspore matures that the nucellus is lengthened five or six times its diameter,

being made up of slightly elongated cells five or six rows thick in median section. The integument, about five cells thick, has now grown well beyond the tip of the nucellus, and its lips have become somewhat appressed to form the long micropyle. The cells in the innermost layer in the integument show active division in the direction of the greatest length of the nucellus, and by their dense protoplasm and large nuclei stand out prominently as a definite layer which I shall designate as the "columnar tissue."

After the disappearance of the megaspore sister cells the definitive megaspore continues its absorptive activity to the destruction of the single layer of nucellus at its micropylar end, so that the distal half of it comes to lie directly against the columnar tissue of the integument. The chalazal end is pointed, occupies at this time a median position in the nucellus, and is apparently active in the degeneration of the nucellar tissue, in accommodation to its own growth. About this time the definitive megaspore undergoes division. The daughter nuclei take places at opposite ends of the embryo sac (*fig. 24*), and quickly undergo the second (*fig. 25*) and third divisions in the normal manner.

The mature embryo sac is typical in every respect. It is elongated to four or five times its width, the sides lie next the columnar tissue and the base continues to be pointed and median. The synergidae lie side by side and the egg protrudes a little way below them, nearer the center of the sac. The cytoplasm of the synergidae is dense and stains heavily with the Flemming triple; that of the egg is greatly vacuolated. The antipodals lie well together in the conical base of the sac (*fig. 26*). The polar nuclei meet midway between the ends of the sac, and after their fusion the endosperm nucleus continues to occupy this position (*fig. 26*). After the fusion of the polar nuclei the endosperm becomes very active in the disorganization of the remaining basal portion of the nucellus. In this activity the antipodals do not take part. The base of the sac remains pointed, but from being median now comes to lie against the columnar tissue at one side of the nucellus by means of the absorption of the nucellar tissue which lay between its previous position and the columnar tissue. The further enlargement of the sac is accompanied by a pushing downward of the base between the nucellus and columnar

tissue, and in some preparations the antipodals would seem to have been pushed to one side (*fig. 27*). The columnar layer now shows its maximum development, being made up of deep, much-flattened cells with darkly staining cytoplasm. The function of these cells is no doubt that of secreting and passing over to the sac sugars or other elaborated foodstuffs.

POLLINATION AND POLLEN TUBES.

Pollination takes place, near Baltimore, during the first week in May. In the mature style of Sarracenia at the time of pollination the umbrella is a pale green color. Its internal structure is leaf-like without a definite palisade, but with abundant intercellular spaces and stomata numerous upon the upper surface and few upon the lower. Long unbranched unicellular hairs cover the lower surface so thickly as to form a tomentum in which considerable pollen is caught at the time of shedding. There are also upon both sides of the umbrella multicellular glands of spheroidal shape projecting slightly above the level of the epidermis. Running from the five stigmatic surfaces toward the center of the umbrella are heavy veins which comprise both vascular and conducting tissue.

The union of the carpels in the formation of the stalk of the style is such as to leave at its center a pentagonal cavity which in the mature flower connects the interior of the capsule with the external air. An examination of the veins of the umbrella two weeks before pollination will show the conducting tissue as a cylindrical strand about ten cells in diameter. The cells are much elongated, with pointed ends, or many cells of this description have divided transversely to two or four cells. The cytoplasm is dense, the nuclei are large, elongated, often three times as wide as long, binucleolate, and poor in chromatin. At the time of the passage of the pollen tubes the conducting strand has become enlarged to more than twice its previous diameter at the expense of the surrounding tissue, and the cells have become still more elongated. The cytoplasm is much vacuolated, the nuclei are attenuate at the ends and devoid of nucleoli (*figs. 32, 33*), and there are large intercellular spaces. The vascular tissue of the veins lies beneath the conducting tissue and is continuous with the vascular tissue of the stylar stalk.

Two weeks before pollination transverse sections of the stalk of the style show five strands of heavy-walled cells running from the angles of the central cavity half way to the periphery (*fig. 34*). The tissue which these cells represent in cross section is four to six cells thick and runs the entire length of the stalk, being in the median line of the carpels. About the time of pollination these sheets of cells are found to split into two layers, which separate in such a manner as to form canals which are connected with the central cavity (*fig. 35*). The surface layer of cells on the interior of the canal becomes detached and undergoes partial degeneration. The five conducting canals thus formed are continuous with the conducting tissue of the veins of the umbrella above, and open below midway between the main placental outgrowths.

The stigmatic surface is richly provided with long, curved, heavy-walled outgrowths of epidermal cells (*fig. 31*), which serve to catch pollen and hold it. Pollen was found to be present in abundance on all stigmas examined. There is no definite sprouting-pore in the grains, but the tubes grow more commonly from the meridional grooves. The pollen tubes grow between the cells of the stigmatic surface and their entire passage is between the cells of the conducting tissue and never through them. They follow the well-defined course of the conducting tissue along the vein of the umbrella and down the stalk of the style (*fig. 30*).

The generative nucleus was not seen in any case to have divided before the sprouting of the pollen tube, and the earliest position in which it was seen to have divided was in a tube which had nearly reached the center of the umbrella. The tube nucleus is spherical and precedes the generative nuclei. The latter are alike in form—elongated and curved or often bent twice in serpentine manner. The distance of the nuclei from the end of the tube is four to six times the diameter of the tube. The cytoplasm is dense in the entire end and around the nuclei (*fig. 36*).

When the pollen tubes enter the cavity of the ovary from the five conducting tubes of the stalk, they are directly above the line of juncture of the two adjacent lateral placental outgrowths. The course of the pollen tubes is at first a downward one between these outgrowths, and later an outward one radial to the axis of the ovary

(*fig. 30*). In this manner the edges of the placentae are reached after a course in the ovary which, for the tubes growing to the lowermost ovules, is as much as 6 to 8^{mm}, and lies entirely outside the tissue of the plant in an ovary the cavity of which has direct communication with the external air. The epidermal cells of the placental surfaces between which the pollen tubes pass are densely filled with cytoplasm; beneath them lie three layers of flattened cells of similar contents. Thin transverse walls are formed in the tubes near the stigmatic surface (*fig. 37*), and far down in the ovary, near the ovules, plugs are not infrequent in the tubes, being three to six times the diameter of the tube in length.

The distance traversed by the pollen tubes which reach the lowermost ovules in flowers of average size, is about 4^{cm}. Provision for the nutrition of the tube during its growth and passage is perhaps made in part by the photosynthetic activity of the umbrella. Previous to pollination the epidermal, subepidermal, and some deeper cells of the umbrella are filled with densely-staining, finely granular contents. In fresh material of the same age the contents of these cells fail to react to tests for sugar made with Fehling's solution, α-naphthol and thymol, as well as to tests for starch. Similar contents fill the epidermal cells of the stalk of the style. The course of the tubes as far as their entrance to the ovary is doubtless through a strong solution of sugars. Below the point of entrance to the ovary the passage between the placental walls is probably through a film of sugary solution held there by capillarity and supplied with materials from the epidermal cells of the placental walls, which after pollination are highly vacuolated, in marked contrast to their condition before pollination.

FERTILIZATION.

The fusion of the male and female nuclei in fertilization is preceded by the division of the endosperm nucleus in nearly all the embryo sacs. Fertilization takes place, then, in all ovules at nearly the same time irrespective of a difference in the development of the endosperm due to the position of the ovule upon the placenta. As to the length of time intervening between pollination and fertilization I am unable to give any exact data. A visit on May 24 to plants

growing in the open found the anthers nearest the ovary to have shed their pollen. Material collected at the same locality two days later was found to show fertilization. The time of pollination of the particular flowers gathered and fixed may have been as much as five days before gathering, but was probably not earlier.

The thin-walled slender pollen tubes may be found in abundance about the mouths of the micropyles, often forming considerable masses. The cells which line the micropyle are heavy-walled and of such darkly-staining contents that it is difficult to observe the pollen tube within the micropyle, and indeed the entrance of the tip of the tube, with the nuclei, was not observed. The synergidae become appressed to the wall of the sac. The end of the tube upon entrance to the sac becomes expanded and pushes downward to one side of the egg. The generative nuclei have lost the elongated shape they were seen to have while passing down the style and have become spherical. Fusion of the first generative nucleus shows no special peculiarities (*fig. 38*).

ENDOSPERM.

The fusion of the polar nuclei is quickly followed by division. The first wall in the endosperm is transverse to the length of the sac and divides it into equal halves (*fig. 39*). The daughter nuclei divide in like manner (*fig. 40*), as do also the grandaughter nuclei, giving rise to an endosperm of eight cells in linear series, in which the walls are all transverse, although not uncommonly somewhat oblique (*fig. 41*). Subsequent divisions are less regular, and by the time the fertilized egg has divided the endosperm contains approximately 150 cells, its base having used up the nucellus either completely or all but a half dozen cells (*fig. 42*). At this time the endosperm cells are highly vacuolated and the laying down of food has not begun.

The relative rate of development of the endosperm in ovules upon different parts of the same placenta is the same as was noted with regard to the integuments. An ovule at the point of juncture of the adjacent lateral placental outgrowths may have an eight-celled endosperm at the same time that the endosperm nucleus has not yet divided in an ovule upon the edge of the placenta nearest the main placental outgrowth.

EMBRYO.

The first division of the fertilized egg is in a direction parallel with the length of the sac. The two-celled embryo (*fig. 43*), at first oval, becomes gradually elongated, divisions following in the same plane as the first, but not in a manner in which it has been possible to discover any regularity. After the embryo has attained a length of five to seven cells, there is a lateral division of the terminal cell (*fig. 44*), the beginning of the embryo proper. The suspensor is usually curved, though not always to so great an extent as shown in the figure. I have been unable by lack of material to observe stages in the development of the embryo immediately following the transverse division of the terminal cell.

In material of June 25 the embryo proper is found to have reached a size of approximately 250 cells, with ellipsoidal form (*fig. 45*). Dermatogen and periblem are well-defined, but no procambial cells have as yet appeared. The endosperm has by this time increased greatly in diameter, encroaching upon the tissue of the integuments. The endosperm cells have become well-stored with aleurone except in the central portion of the micropylar end—the region destined to be occupied by the full-sized embryo of the mature seed. In embryos as large as that shown in *fig. 45* the suspensor is surrounded by endosperm cells in which aleurone has been laid down; the embryo proper is surrounded by cells of highly vacuolated contents.

SEED AND SEEDLING.

Material gathered during the last week of July exhibits seeds which are practically mature. The embryo has grown to an elongated ellipsoidal form, the cotyledons being about one-third the length of the whole (*fig. 46*). Elongated procambium cells stretch from the basal end of the embryo to the region of the stem growing-point. Stomata are not formed in the embryo until the time of germination. A few endosperm cells at the sides and cotyledonary end of the embryo are free of aleurone, as they remain in the mature seed.

The surface layer of cells of the integument forms the seed coat. Its cells become irregular on their external surface and the walls are greatly thickened, with conspicuous pores in the lateral and basal walls, but none in the walls forming the surface of the seed

(*fig. 47*). The inner cells of the integument are all disorganized by the growth of the endosperm and reduced to a layer of the remaining walls of flattened cells. The raphe of the ovule develops into a wing upon one side of the seed, as seen in *fig. 47*. In the mature seed there is a coating of wax upon the surface which renders them unwettable, a condition in which they remain for several weeks after they have been placed in wet moss.

Provision for the shedding of the seed is made by a deep furrow surrounding the raphe just at its junction with the placenta (*fig. 48*). The dehiscence of the capsule is loculicidal and is provided for by a deep suture upon the external surface of the capsule wall at a point where the wall is traversed by a heavy vascular bundle. Dehiscence takes place late in September or early in October, the seeds are scattered gradually during many weeks by chance shaking of the scape by wind or animals. The old flower, with umbrella and sepals still persisting, is often found side by side with the bloom of the following year.

On germination the seed is elevated above the soil or moss by growth of the hypocotyl, which is sharply bent and is the first part of the seedling to protrude. The tips of the cotyledons remain for some time in the seed, functioning as haustoria for the removal of the stored food of the endosperm. The tips of the cotyledons are active in the removal of the endosperm both at their ends and along their sides (*fig. 49*). The cotyledons expand to liguliform leaves about 1 cm long (*fig. 50*), and persist until about the time of the formation of the third epicotyledonary leaf. The cotyledons develop stomata during the process of germination and the epidermal and subepidermal layers of isodiametric cells bear chlorophyll.

DEVELOPMENT OF LEAVES.

The stem growing-point of Sarracenia is massive and acutely dome-shaped in the seedling (*fig. 51*). There is a definite layer of dermatogen and a common group of initials for periblem and plerome. The first epicotyledonary leaf arises opposite the interval between the cotyledons. It is finger-shaped with a somewhat broadened base. On reaching a length about twice its diameter there begins a rapid lateral outgrowth of the tissue of an O-shaped area on the

side of the leaf rudiment which faces the growing-point, giving rise to a pit which is destined to become the cavity of the pitchered leaf (*fig. 52*). The basal part of the **0**-shaped outgrowth now begins to grow upward, in which it is accompanied at the same rate by the upper portion of the **0**, which at the same time carries forward the apical growth of the leaf (*fig. 53*). The cavity of the pitcher thus grows in depth by the upward growth of the tissue by which it is surrounded. The bottom of the cavity is subsequently elevated to some extent by the further growth of the tissue beneath it, but there is no sinking of the bottom of the cavity, considered as a possibility by ZIPPERER.[2] The entire early development of the leaf resembles closely that which has been described for *Darlingtonia californica* by GOEBEL.[3]

The first epicotyledonary leaf reaches its maximum size at a length of about 2.5^{cm}, and is slender in form, the cavity reaching well down toward its base, and the wing being but slightly developed. At the summit it is hooded in such a manner as to resemble the mature leaf of *S. variolaris*. The walls of the pitchers of the seedling are six to eight cells in thickness, with open mesophyll, chlorophyll in all the cells, and stomata over the entire external epidermis. There are two principal strands of vascular tissue, one in the base of the wing and one on the opposite side of the pitcher, with smaller anastomosing strands between these. In the throat of the pitcher all the epidermal cells are produced into long projecting points; lower in the pitcher occasional epidermal cells, smaller than the others, give rise to long heavy-walled hairs, while in the bottom of the pitcher the epidermal and first layer of subepidermal cells are small and heavy-walled.

While each leaf of the young plant is passing through its period of most active growth, the internode between it and the next lower leaf is also elongating rapidly. A young leaf appears for this reason to arise from the petiole of the leaf below it (*fig. 51*). The relative elongation of the internodes is far greater in the seedling than in the adult plant.

The growth of a single plant from seedling to adult was not fol-

[2] Beitrag zur Kenntniss der Sarraceniaceen. Inaug. Diss. Erlangen. 1885.

[3] Pflanzenbiologische Schilderungen II. **5**:73–92. *pls. 19–21*. 1893.

lowed, but evidence points to the time requisite for the seedling to reach blooming age as being five or six years. Seeds of the crop of 1901, which in October of that year were placed in sphagnum in a loosely covered glass vessel, germinated in July 1902, and now, after 33 months, have no pitchers measuring over 2^{mm} in diameter. The extremely artificial conditions under which these seedlings were kept would make it inadvisable, however, to draw from them any general conclusions as to the rate of growth in the seedlings under natural conditions. The great number of intermediate stages in growth between the seedling and adult which may be observed in a single locality at any one season would also argue for the slowness of the plant in reaching adult size.

The stem growing-point of the adult plant is more broadly dome-shaped than that of the seedling, but is identical with it in the mode of origin of the dermatogen, periblem, and plerome. The earliest primordium of the leaf is likewise more massive than in the seedling, but essentially similar. Its form is conical, with a broadly semi-circular base embracing the growing-point. Near the summit, upon the side toward the growing point, is developed the narrow pit which is destined to form the cavity of the pitcher, its origin being due wholly to a difference in the rate of growth of the tissue at the bottom of the pit and that forming its sides (*fig. 54*). BAILLON[4] in a brief note on the development of a Sarracenia (species not mentioned) has described this early stage and called attention to its similarity to an early stage in the development of peltate leaves, averring that "La membrane qui tapisse intérieurement l'urne n'est autre chose que l'épiderme supérieur de la feuille." This may be an entirely superficial analogy, or it may be a hint as to the ultimate origin of such a markedly modified leaf. GOEBEL (*l. c.*) has figured the early leaf primordium of *S. Drummondii*, which is essentially like that of *S. purpurea*.

With the continued growth of the leaf rudiment the pit becomes deeper, and its mouth becomes vertically elongated, although remaining very narrow. At stages somewhat earlier than that shown in *fig. 55*, the sides of the mouth of the pit have come together, closing it completely. *Fig. 55* represents a leaf primordium in which

[4] (Note on the development of leaf of Sarracenia) Adansonia **9**:380. 1870.

the wing is just beginning to appear. *Figs. 56–61* represent cross sections of the primordium at this age in the places indicated in *fig. 55*.

In older leaves, such as are represented in *fig. 62*, the base of the leaf primordium is stoutly crescentic in cross section. Through the groove at the inner side of the leaf base the next younger leaf appears (*figs. 55* and *62*). The groove becomes narrower and more shallow as we pass up the leaf and ends just short of the bottom of the cavity of the pitcher (*fig. 62*). Above the end of the groove there is a short portion of the young leaf which is circular in cross section, above which in turn the narrow flattened outgrowth of the wing has become more conspicuous. The wing rudiment ends rather abruptly at a point where retardation of growth in diameter indicates the line of demarcation between the pitcher and cover. The cavity of the pitcher at this stage reaches as far as the upper end of the circular portion of the base.

There have been many suggestions as to the homology of the parts of the pitchered leaf of Sarracenia. A view held by many is that the pitchered portion of the leaf is derived from the primordium of the petiole and the cover from the primordium of the lamina. GOEBEL (*l. c.*) points out that since there can be no distinction in the very young leaf of primordia of petiole and lamina there can be no line drawn as to what portions of the pitchered leaf "represent" these structures.

The anatomy of the mature leaf was first worked out by VOGL;[5] it has more recently been reviewed by GOEBEL (*l. c.*), and minor contributions have been made by SCHIMPER[6] (1882) and ZIPPERER (*l. c.*). The first leaf rudiments unfolded in the spring are aborted (*fig. 62*), consisting of the sheathing base surmounted by the minute retarded primordium of pitcher and cover. These are usually three in number, and may occur in plants which do not bloom, as well as in those which do. In the latter case the aborted leaves are those just above the one to which the flower appears to be axillary.

[5] Die Blätter der *Sarracenia purpurea*. Sitzungsb. Wiener Akad. Wiss. Math.-Naturw. **50**:281-301. *pls. 2*. 1864.

[6] Notizen über insectfressende Pflanzen. Bot. Zeit. **40**:225–234, 241–248. *pl. 4* (*figs. 1–3*). 1882.

The axillary buds of Sarracenia are commonly very small and consist of growing-point and the primordium of a single leaf, completely covered and protected by the sheathing leaf base. An occasional axillary bud develops, the first two leaves being opposite and on the opposite sides of a line connecting the growing-point of the bud with the center of the shoot. There is thus brought about a branching of the rhizome, which by frequent repetition gives rise to large clusters of individuals.

The anatomy of the rhizome of *S. purpurea* has been described by ZIPPERER in sufficient detail, since it presents no unusual fatures. He has also given a correct account of the growing-point of the root and the development of the vascular tissue of the root: the growing-point being of the type in which the cap and three tissue layers are all derived from a common group of initials; the early order of vascular bundles being triarch.

Root hairs are few upon the roots of plants growing in a saturated substratum in the open, but are abundant in seedlings grown in highly saturated sphagnum, and in adult plants in the open which are growing in a substratum merely moist. Mycorhiza has not been observed in *S. purpurea* in the vicinity of Baltimore, although fungal threads have been found covering the root of seedlings grown under the conditions previously mentioned and penetrating the epidermis. MACDOUGAL[7] (1899) has described penetration of the epidermis by hyphae in adult plants without committing himself as to their mycorhizal nature.

SUMMARY.

1. The flowers of *Sarracenia purpurea* are axillary, perfect, hypogynous, and radially symmetrical. The stamens are seventy to eighty in number and arise in ten groups. There are four microsporangia. There is a double layer of binucleate tapetal cells, derived from the primary archesporium. There are three to five parietal layers. The tetrad division is simultaneous; the microspore nucleus divides before the dehiscence of the anthers. The reduced number of chromosomes is twelve.

2. In the ovule there is a single archesporial cell, which is the megaspore mother cell. There is no tapetal cell. The ovule is

[7] Symbiotic saprophytism. Annals of Botany 13:1–47. 1899.

anatropous and there is a single integument. The megaspore mother cell divides to a linear series of four megaspores, or after the first division the micropylar nucleus may fail to divide or may divide by a wall longitudinal to the ovule.

3. The chalazal megaspore is functional, and develops a typical eight-celled embryo sac. The polar nuclei fuse and the endosperm may become two to eight-celled before the complete fusion of male and female nuclei in fertilization.

4. The pollen tube grows through a definite conducting tissue in the upper expanded portion of the style, through schizogenic canals in the stalk of the style and between the placental outgrowths in the ovary. The generative nucleus divides before the tube has passed into the stalk of the ovary. Fertilization presents no peculiarities.

5. The embryo is elongated and straight, with cotyledons. The storage tissue is endosperm filled with aleurone. The seed coat is the external layer of the integument. The cotyledons function as haustoria in germination and survive as chlorophyl-bearing leaves.

6. The first epicotyledonary leaf is pitchered and arises from a finger-like primordium in which a cavity is developed by unequal growth.

THE WOMAN'S COLLEGE OF BALTIMORE,
Baltimore, Md.

EXPLANATION OF PLATES III–V.

Abbreviations used: *ant*, antipodal; *arsp*, archesporium; *br*, bract; *cav*, cavity; *col t*, columnar tissue; *con c*, conducting canal; *con s*, conducting strand; *con t*, conducting tissue; *cot*, cotyledons; *cov*, cover; *cp*, carpel; *der*, dermatogen; *d s*, dehiscing slit; *e*, egg; *em*, embryo; *en n*, endosperm nucleus; *e s*, embryo sac; *esp*, endosperm; *f n*, female nucleus; *g n*, generative nucleus; *int*, integument; *int i*, integument initials; *l*, leaf; *l p o*, lateral placental outgrowth; *meg mc*, megaspore mother cell; *meg sc*, megaspore sister cell; *mic mc*, microspore mother cell; *micsp*, microsporangium; *mn*, male nucleus; *m p o*, main placental outgrowth; *nuc*, nucellus; *ov*, ovary; *par c*, parietal cells; *pet*, petals; *pn*, polar nuclei; *ppi*, initials of periblem and plerome; *pro c*, procambium cells; *sc*, seed coat; *sep*, sepal; *st*, stamen; *stg s*, stigmatic surface; *stk*, stalk of style; *sus*, suspensor; *syn*, synergid; *tap c*, tapetal cells; *tn*, tube nucleus; *um*, umbrella of the style; *w*, wing.

All figures are camera drawings fom microtome sections except *figs. 29, 30, 50, 55,* and *62*, which are from free-hand drawings.

PLATE III.

FIG. 1. Vertical section of young flower bud. ×30.

FIG. 2. Transverse section of young flower bud of same age as in *fig. 1;* dotted outline represents position of carpel tips in higher sections. ×30.

FIG. 3. Vertical section of older flower bud. ×30.

FIG. 4. Transverse section of young stamen. ×232.

FIG. 5. Transverse section of single microsporangium of older stamen. ×232.

FIG. 6. Tranverse section of portion of microsporangium and wall in microspore mother cell stage. ×400.

FIG. 7. Transverse section of portion of microsporangium and wall with microspore mother cells in synapsis. ×232.

FIG. 8. Transverse section of mircosporangium and portion of wall; pollen mother cells in mitosis. ×400.

FIG. 9. Pollen mother cells in metaphase of first mitosis. ×400.

FIG. 10. Tetrads of microspores. ×400.

FIG. 11. Pollen grain. ×400.

FIG. 12. Pollen grain after division of nucleus. ×400.

FIG. 13. Transverse section of mature anther. ×20.

FIG. 14. Transverse section of young ovary. ×20.

FIG. 15. Transverse section through middle of nearly mature ovary. ×7.

FIG. 16. Longitudinal section of ovule with megaspore mother cell. ×400.

FIG. 17. Transverse section of ovule through megaspore mother cell. ×400.

FIG. 18. Longitudinal section of ovule with megaspore mother cell and integument. ×232.

FIG. 19. Transverse section of single lateral placental outgrowth, showing difference in rate of development of integument on different parts of the placenta; somewhat diagrammatic. ×40.

PLATE IV.

FIG. 20. First maturation division of megaspore mother cell. ×400.

FIG. 21. Linear series of three megaspores, arising by failure of micropylar daughter cell to divide. ×400.

FIG. 22. Tetrad of megaspores in which the micropylar daughter cell has divided longitudinally. ×400.

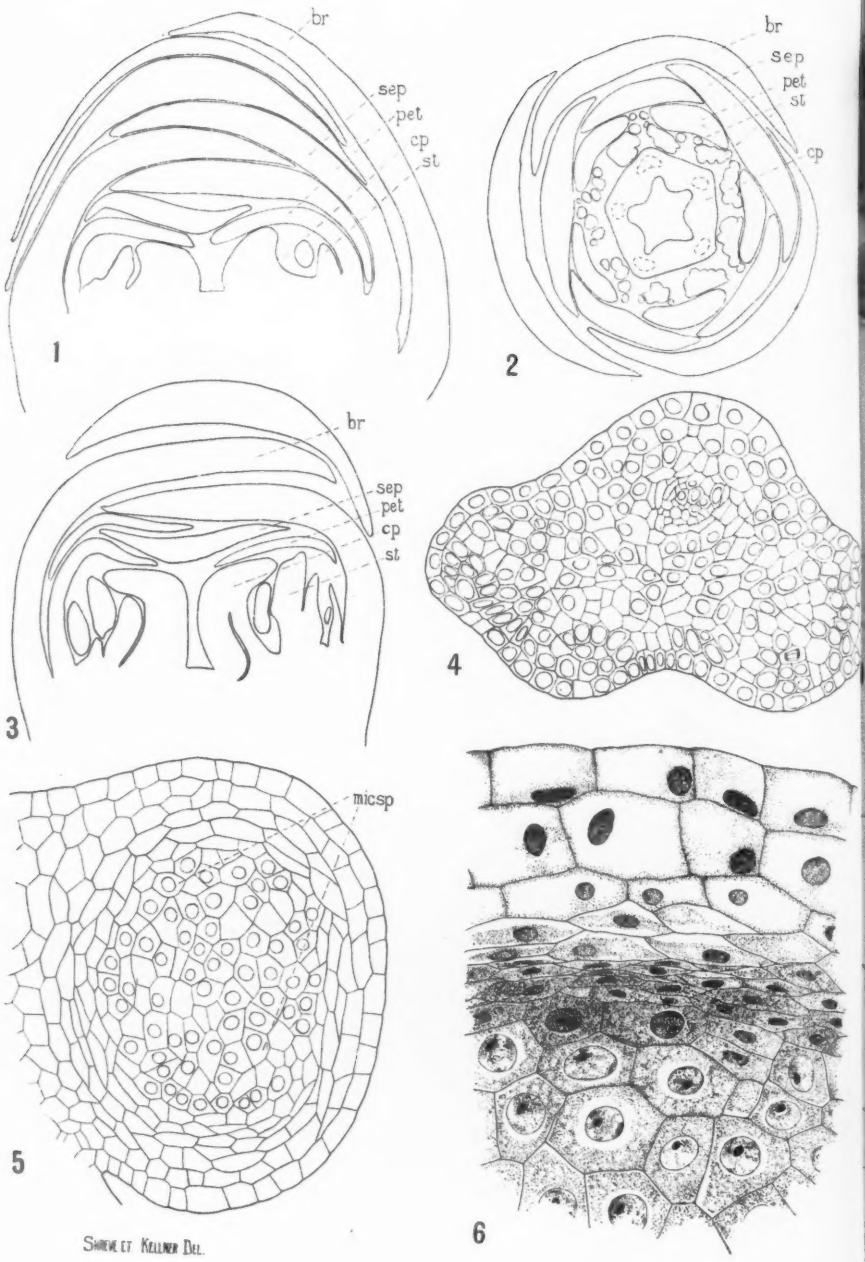
FIG. 23. Longitudinal section of ovule, with tetrad of megaspores, chalazal one enlarging and encroaching on single layer of nucellus. ×120.

FIG. 24. Longitudinal section of portion of ovule showing two-celled embryo sac, nucellus, and columnar tissue. ×232.

FIG. 25. Longitudinal section of portion of ovule showing four-celled embryo sac. ×232.

FIG. 26. Longitudinal section of portion of ovule showing fully developed embryo sac. ×400.

FIG. 27. Longitudinal section of portion of ovule showing embryo sac after fusion of polar nuclei; antipodals pushed to one side. ×232.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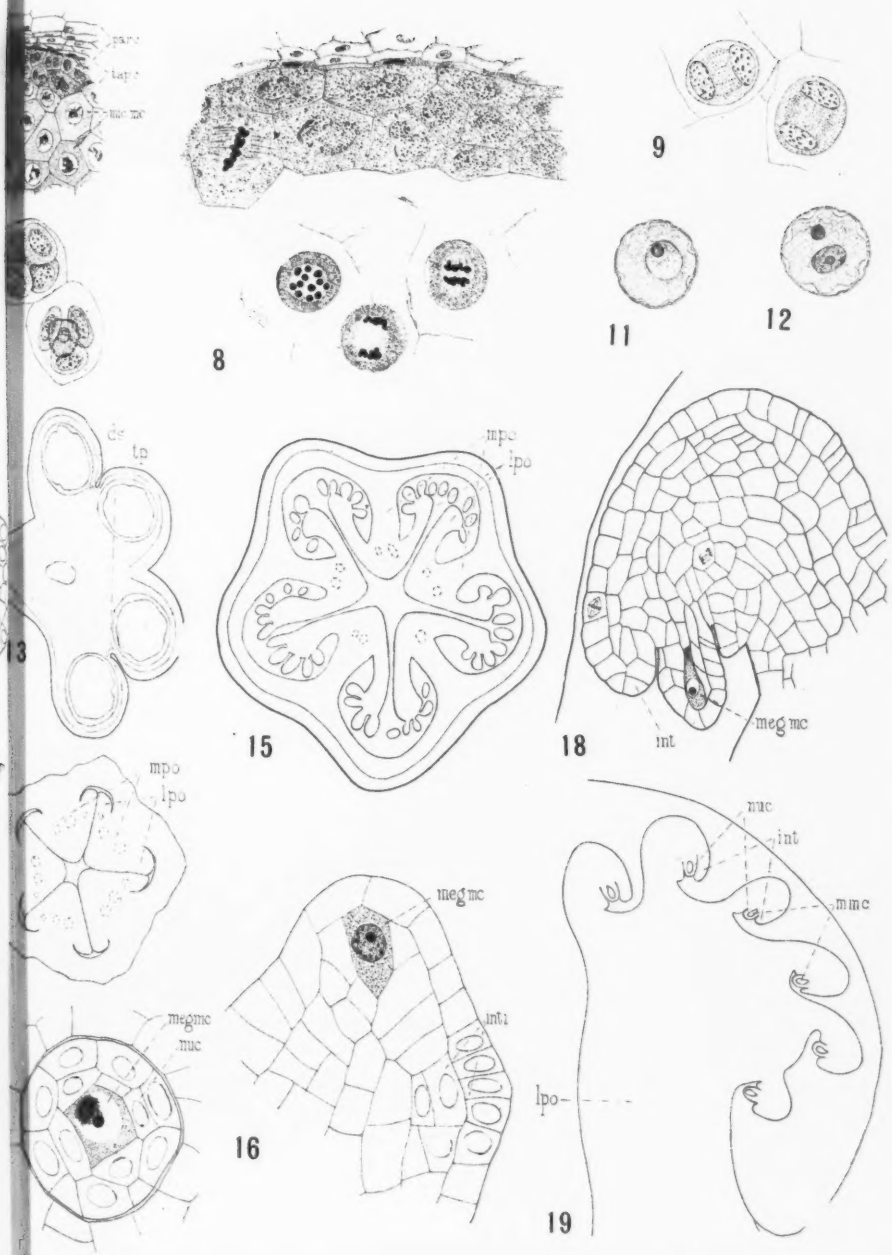
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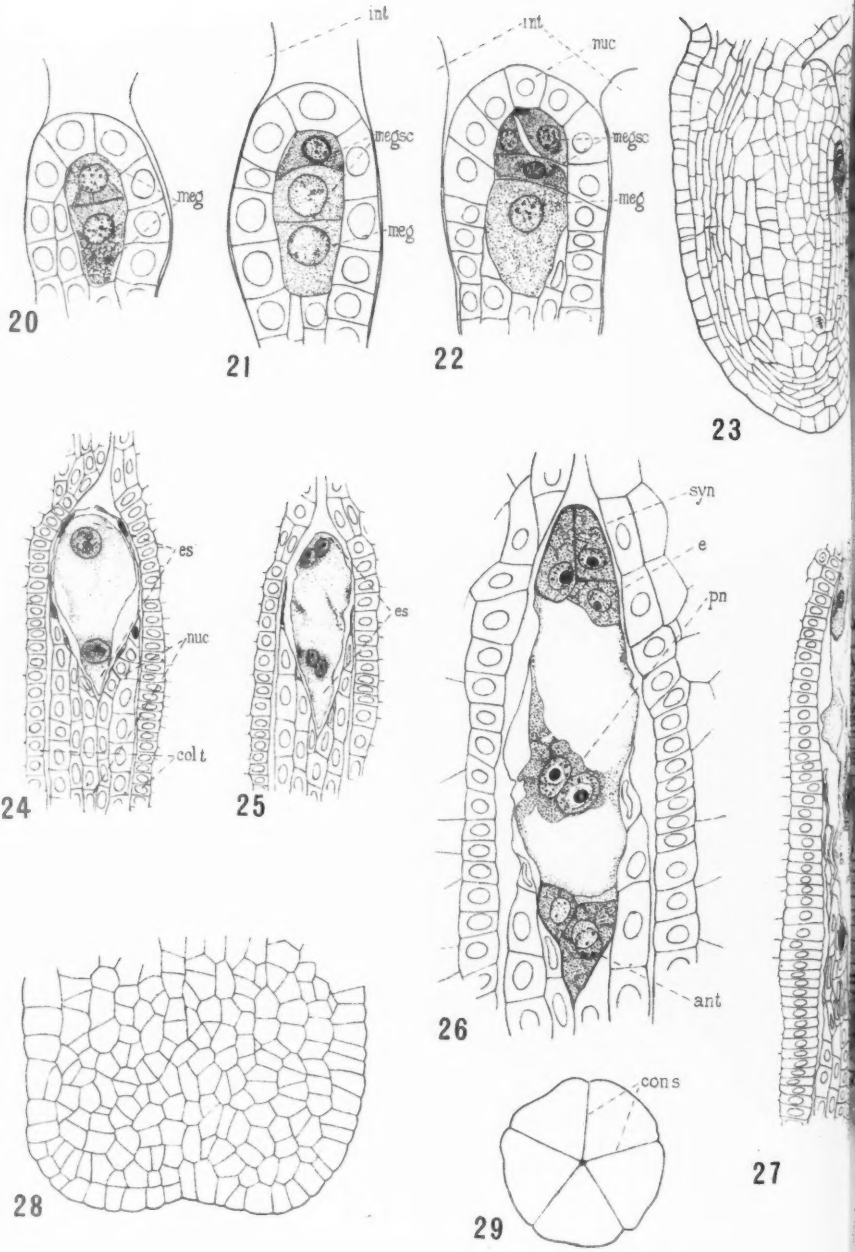
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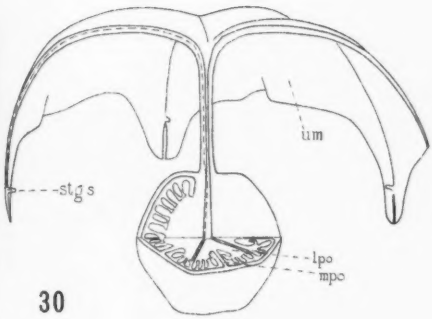

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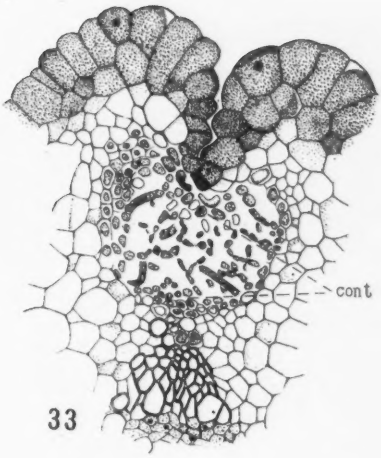

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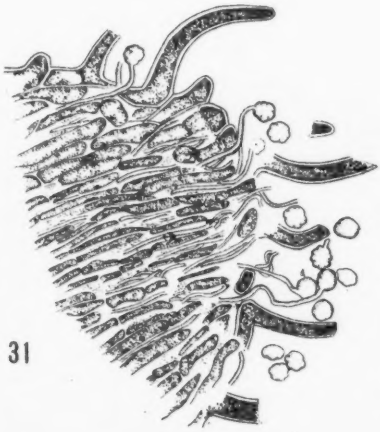

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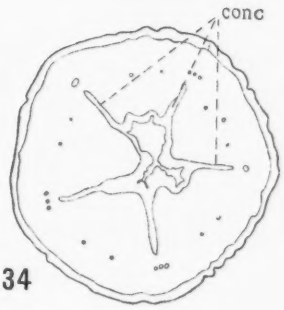

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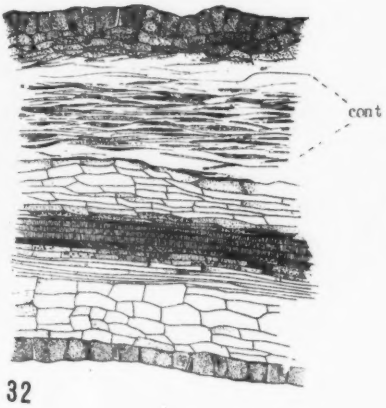

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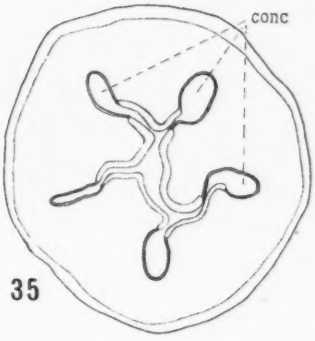

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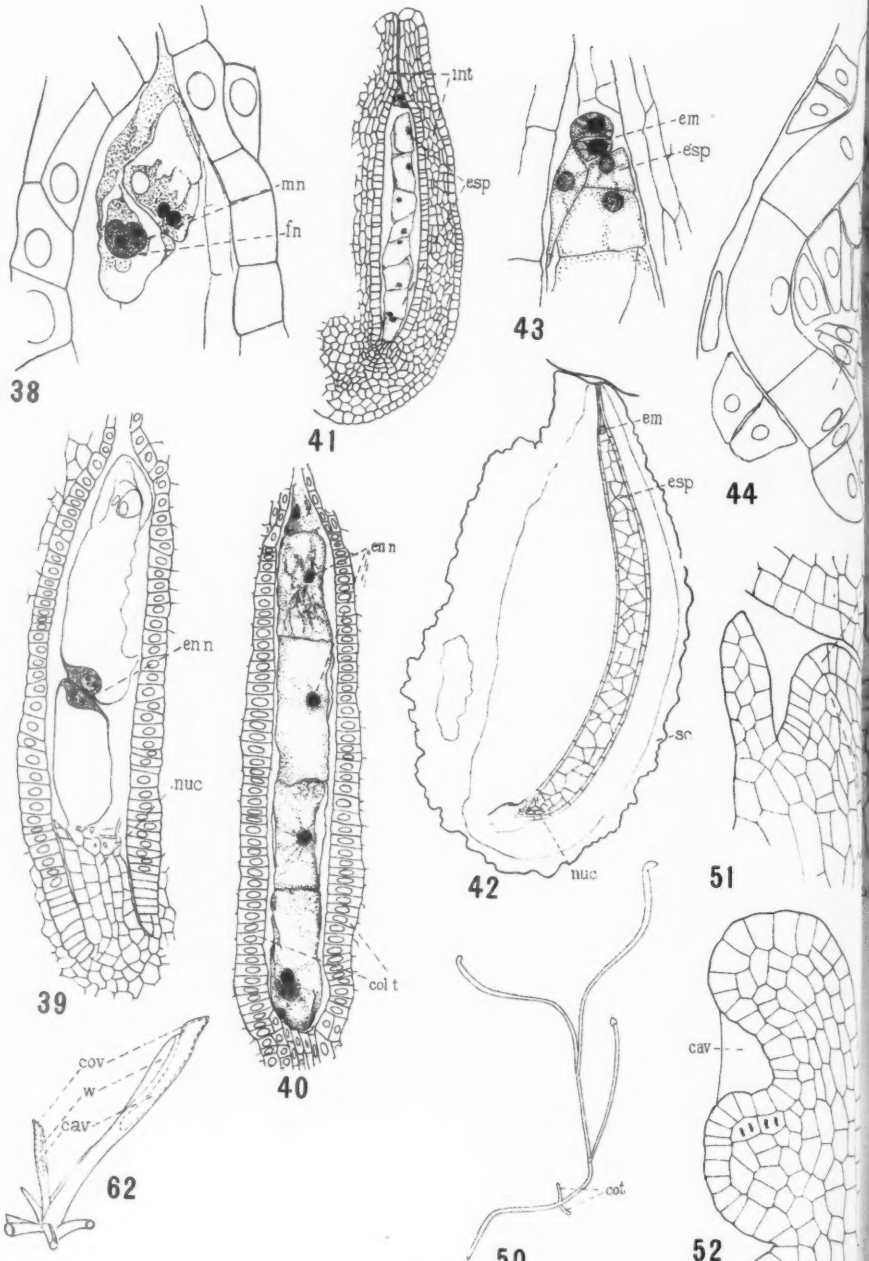
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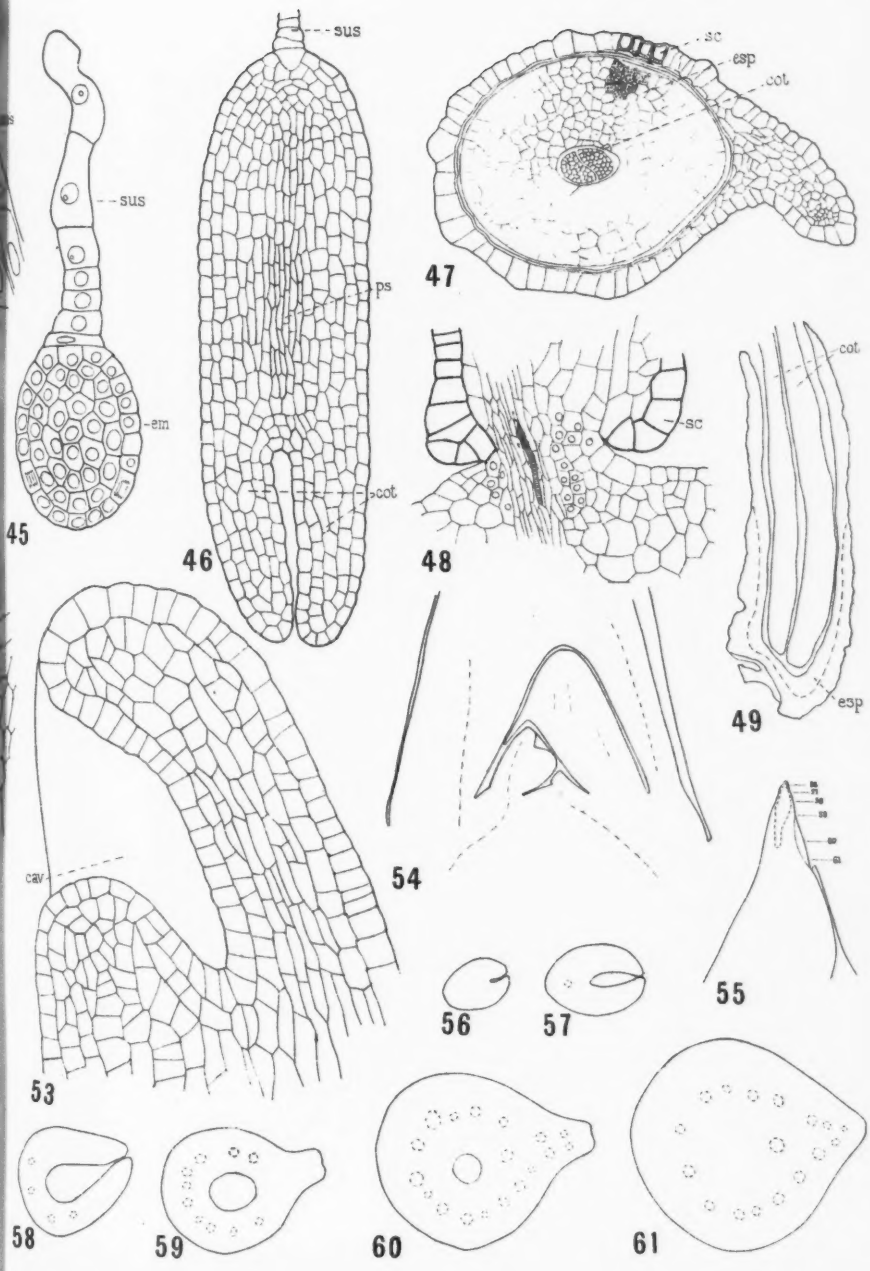
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FIG. 28. Growing point of tip of carpel in umbrella, horizontal section. ×40.

FIG. 29. Stylar umbrella viewed from above; in outline. ×$\frac{2}{3}$.

FIG. 30. Ovary and style to show the course of pollen tube indicated by dotted line; somewhat diagrammatic. ×2.

FIG. 31. Longitudinal section of stigmatic surface with sprouting pollen grains. ×120.

FIG. 32. Longitudinal section of conducting strand in umbrella of style showing conducting and vascular tissue. ×40.

FIG. 33. Transverse section of upper surface of umbrella of style showing conducting and vascular tissue and glandular epidermis. ×120.

FIG. 34. Transverse section of stalk of style before pollination. ×20.

FIG. 35. Transverse section of stalk of style at time of pollination. ×20.

FIG. 36. Tip of pollen tube from conducting tissue of umbrella; optical section. ×400.

FIG. 37. Cross wall in tube near stigmatic surface. ×400.

PLATE V.

FIG. 38. Longitudinal section of upper end of embryo sac showing fusion of male and female nuclei. ×400.

FIG. 39. Longitudinal section of embryo sac showing two-celled endosperm, columnar tissue, and remains of nucellus. ×120.

FIG. 40. Longitudinal section of embryo sac showing four-celled endosperm. ×120.

FIG. 41. Longitudinal section of portion of ovule showing eight-celled endosperm and integument. ×40.

FIG. 42. Longitudinal section of seed through the wing showing multicellular endosperm and two-celled embryo. ×20.

FIG. 43. Two-celled embryo. ×232.

FIG. 44. Young embryo with suspensor. ×400.

FIG. 45. Older embryo with suspensor. ×232.

FIG. 46. Longitudinal section of embryo from mature seed. ×120.

FIG. 47. Tranverse section of mature seed cutting the embryo through the cotyledons; detail partially filled in. ×40.

FIG. 48. Longitudinal section through the hilum of nearly mature seed. ×120.

FIG. 49. Longitudinal section of germinating seed, with cotyledons; seed coat has been removed; portion beyond the dotted line is that from which aleurone has not yet been removed. ×20.

FIG. 50. Seedling with cotyledons and three epicotyledonary leaves. ×1.5.

FIG. 51. Vertical section through growing-point of seedling. ×232.

FIG. 52. Median vertical section through primordium of first epicotyledonary leaf. ×232.

FIG. 53. Median vertical section through portion of primordium of first epicotyledonary leaf in later stage of development. ×232.

FIG. 54. Vertical section through growing point and young leaves in adult plant. ×20.

FIG. 55. Surface view of primordium of leaf seen from the side, next younger leaf also showing; dotted outline marks cavity of leaf. ×3.

FIG. 56. Transverse section of leaf in *fig. 55* at *56*. ×20.

FIG. 57. Transverse section of leaf in *fig. 55* at *57*. ×20.

FIG. 58. Transverse section of leaf in *fig. 55* at *58*. ×20.

FIG. 59. Transverse section of leaf in *fig. 55* at *59*. ×20.

FIG. 60. Transverse section of leaf in *fig. 55* at *60*. ×20.

FIG. 61. Transverse section of leaf in *fig. 55* at *61*. ×20.

FIG. 62. Later stages of young leaves; cavities shown by dotted outline. ×1

ON THE IMPORTANCE OF PHYSIOLOGICALLY BALANCED SOLUTIONS FOR PLANTS.[1]

I. MARINE PLANTS.

W. J. V. OSTERHOUT.

RINGER demonstrated that animal tissues live longer in a solution of NaCl to which a small amount of KCl and $CaCl_2$ is added than in a solution of NaCl alone. Various explanations of this fact were given by different investigators, all of whom, however, agreed upon the essential point that KCl and $CaCl_2$ are essential for the maintenance of life.

HOWELL assumed that $CaCl_2$ is the stimulus for the heart beat, while NaCl is an indifferent substance, necessary only for the maintenance of osmotic pressure. Similarly RINGER concluded that Ca is the stimulus for the systole, while K is necessary for the diastole of the heart beat.

HERBST made experiments on the influence of the composition of the sea water on sea urchin eggs, eliminating in each successive experiment a different constituent of the sea water. He found that the eggs would not develop in any solution which did not contain all the salts of the sea water. From this he concluded that each of the salts found in sea water is necessary for the development of the egg. LOEB called this view in question as the result of his experiments on Fundulus. He found that this marine fish cannot live in a pure NaCl solution of the same osmotic pressure as the sea water, but that it can live indefinitely in a mixture of NaCl, KCl, and $CaCl_2$, in the same proportions in which these salts are contained in sea water. The fish can also live indefinitely in distilled water. This proves that it does not need any of the three salts mentioned for the maintenance of its life, and that the Ca and K are only required to overcome the poisonous effects which would be produced by the NaCl if it alone were present in the solution (at the above mentioned concentration).

[1] I wish here to express my sincere thanks to Professor LOEB, who kindly placed the facilities of his laboratory at my disposal and assisted me in every way during these investigations.

It is noteworthy that the Ca and K, which are added to inhibit the toxic effect of NaCl, are themselves poisonous at the concentration at which they are here employed.

These antagonistic effects of Ca and K toward a pure NaCl solution were illustrated still more strikingly in experiments on the egg of Fundulus. The newly fertilized eggs of this fish develop equally well in sea water and in distilled water, but die in a pure $m/2$ NaCl solution without forming an embryo. If, however, a small but definite amount of a salt with a bivalent kation, even of such poisonous salts as $BaCl_2$, $ZnSO_4$, and $Pb(CH_3\text{-}COO)_2$, is added, the eggs will produce embryos. From these and similar observations LOEB was led to formulate his conception of the necessity of physiologically balanced salt solutions, in which are inhibited or counteracted the toxic effects which each constituent would have if it alone were present in the solution.

The blood, the sea water, and to a large extent RINGER'S solution, are such physiologically balanced salt solutions. The observations of HERBST, as well as those of RINGER, are easily explained on this basis. The fact that the elimination of any one constituent from the sea water makes the solution unfit to sustain life does not prove that the eliminated substance is needed by the animal for any purpose other than to counteract the poisonous action of some other constituent of the solution.

Botanists have not thus far made use of these conclusions, for the obvious reason that facts similar to those mentioned above have not been observed in plants. I have recently made a number of experiments which show that there exist in plants phenomena similar to those observed by LOEB on Fundulus and other marine animals.

The species of marine plants chosen for investigation may be divided into two groups:

Group 1 comprises plants which can live a long time in distilled water. It includes the following: BLUE-GREEN ALGAE, Lyngbya aestuarii; GREEN ALGAE, Enteromorpha Hopkirkii; FLOWERING PLANTS, Ruppia maritima.

Group 2 is composed of plants which quickly die in distilled water. It includes the following: GREEN ALGAE, Enteromorpha intestinalis; BROWN ALGAE, Ectocarpus confervoides; RED ALGAE,

Ptilota filicina, Pterosiphonia bipinnata, Iridaea laminarioides, Sarcophyllis pygmæa, Nitophyllum multilobum, Porphyra naiadum, Porphyra perforata, Gelidium sp., Gymnogongrus linearis, Gigartina mammillosa.[2]

If plants of either group be placed in a solution of pure sodium chlorid (isotonic with sea water), they die in a short time. This might be attributed to the lack of certain salts which are necessary for their metabolism, rather than to the toxicity of the sodium chlorid. In the case of the plants of Group 1 there can be no doubt on this point, for these plants live a long time in distilled water. If we add pure sodium chlorid to the distilled water it kills them in a very short time. An inspection of the tables will show that these plants in their behavior toward sodium chlorid and other salts, closely agree with those of Group 2, which can live but a short time in distilled water. Sodium chlorid is certainly toxic to the first group, and there can be little doubt that it is so to the second group as well.

The plants of the first group were found in a ditch in a salt marsh through which the tide ebbs and flows; there is always a foot or so of water even at low tide. The salt content of the water fluctuates around a mean of approximately 2.3 per cent.

The plants of the second group were collected at the entrance to San Francisco Bay, where the salt content of the water fluctuates about a mean which is probably not far from 2.7 per cent. The only exceptions are *Enteromorpha intestinalis* and *Ectocarpus confervoides*, which came from wharves in the bay, where the mean salt content is about 2.3 per cent.

All the plants used in the experiments were transferred from the sea water directly to distilled water. After rinsing in this they were placed in glass dishes, each containing 200^{cc} of the solution to be tested. The dishes were then covered with glass plates to exclude dust and check evaporation. Only a small amount of material was placed in each dish. The temperature during the experiments did not vary far from 18° C.

Artificial sea water was prepared[3] according to VAN 'T HOFF'S

[2] The determinations were kindly made by Professor SETCHELL.

[3] The water used was distilled in glass only and the first part of the distillate rejected. The purity of each salt was carefully tested before using.

formula[4] as follows: 1000^{cc} NaCl, $3m/8$; 78^{cc} $MgCl_2$, $3m/8$; 38^{cc} $MgSO_4$, $3m/8$; 22^{cc} KCl, $3m/8$; 10^{cc} $CaCl_2$, $3m/8$.[5]

This closely approximates the bay water. The plants thrive almost as well in it as in sea water, especially when a very little $NaHCO_3$ or $KHCO_3$ is added to produce a neutral or faintly alkaline reaction.

A series of solutions was tried, beginning with pure NaCl $3m/8$ and adding to it in turn $MgCl_2$, KCl, and $CaCl_2$, either singly or in combination, in the proportions given above. These salts were also used in pure solutions of the same concentration at which they exist in the artificial sea water described above.

It should be said that little difficulty was experienced in determining the death point with sufficient precision. The color reactions and the microscopic appearance of the cells allowed this to be done with sufficient accuracy, so that the results were not in doubt on this account.

The results of the experiments are set forth in the tables. The figures represent the average of four parallel series carried on simultaneously. A control series was also carried on in which each solution was made faintly alkaline by the addition of $NaHCO_3$, $KHCO_3$, or $Ca(OH)_2$. This had a beneficial effect during the first two or three days of the experiment, but the final results were practically the same as in the other series.

From a consideration of the results for Group 1 we may draw the following conclusions.

1. The plants die much sooner in a pure sodium chlorid solution (isotonic with sea water) than in distilled water. The poisonous effect of the NaCl largely disappears if we add a little $CaCl_2$ (10^{cc} $CaCl_2$ $3m/8$ to 1000^{cc} NaCl $3m/8$); in this mixture the plants live nearly as long is in distilled water. Addition of KCl to this mixture enables them to live longer than in distilled water. Further addition of $MgCl_2$ and $MgSO_4$ enables them to live practically as long as in sea water.

[4] VAN'T HOFF, J. H., Physical chemistry in the service of the sciences 101. Univ. of Chicago Press, 1903.

[5] This corresponds approximately to the proportion of Ca in the sea water of the bay.

TABLE I.

Duration of Life in Days.

Culture solution.	Group 1			Group 2		
	Lyngbya aestuarii	Enteromorpha Hopkirkii	Ruppia maritima	Ptilota filicina	Pterosiphonia bipinnata	Iridæa laminarioides
Sea water (total salts 2.7 %)	95	150+	150+	11	24½	24
Artificial sea water: 1000 cc NaCl 3m/8, 78 " $MgCl_2$ ", 38 " $MgSO_4$ ", 22 " KCl ", 10 " $CaCl_2$ "	90	150+	150+	10½	24½	23
Distilled water	30	30	80	1	3½	2½
Tap water	32+	36	85	2½	9½	10
NaCl 3m/8	22	15	23	1¼	3½	4
1000 cc NaCl ", 10 " $CaCl_2$ "	29	23	65	2½	6	5
1000 " NaCl ", 22 " KCl ", 10 " $CaCl_2$ "	35	32	88	3½	10	9
1000 " NaCl ", 78 " $MgCl_2$ ", 10 " $CaCl_2$ "	29	23	45	3	6	6
1000 " NaCl ", 78 " $MgCl_2$ ", 22 " KCl "	25	13½	30	2	4	4
1000 " NaCl ", 22 " KCl "	23	13½	23	1	2	5
1000 " NaCl ", 78 " $MgCl_2$ "	22⅝	13½	25	1½	2	2
1000 " Dist. H_2O, 78 " $MgCl_2$ "	15½	16½	19	1	2	2¼
1000 " Dist. H_2O, 38 " $MgSO_4$ "	17½	13	23	1	2	2
1000 " Dist. H_2O, 22 " KCl "	21	13½	56	1	1⅝	5⅓
1000 " Dist. H_2O, 10 " $CaCl_2$ "	26+	12½	58	2½	5	2

TABLE II.

DURATION OF LIFE IN DAYS. GROUP 2.

CULTURE SOLUTION.	Enteromorpha intestinalis	Ectocarpus confervoides	Sarcophyllis pygmæa	Nitophyllum multilobum	Porphyra naiadum	Porphyra perforata	Gelidium sp.	Gymnogongrus linearis	Gigartina mammillosa
Sea water (total salt 2.7 %)	240	25	11	4½	6	21	33+	11	11
Artificial sea water: 1000 cc NaCl 3m/8, 78 " $MgCl_2$ ", 38 " $MgSO_4$ ", 22 " KCl ", 10 " $CaCl_2$ "	220	20	7½	4½	6	20	33+	10	9¼
Distilled water	3	1¼	1⅝	2½	2½	3⅓	1⅝	2½	3½
Tap water	10	2¼	3¾	3¾	2½	4½	5½	4½	5¼
NaCl 3m/8	4¾	⅔	1⅔	⅝	2⅛	3	3	5⅚	2½
1000 cc NaCl ", 22 " KCl ", 10 " $CaCl_2$ "	68	8	5½	3½	5	14⅛	33+	9	6
1000 " Dist. H_2O, 22 " KCl "	4¾	4	1⅝	..	4¾	3	3	4	3

2. The pure solution of each of the salts added to inhibit the poisonous effects of NaCl is itself poisonous at the concentration at which it exists after its addition, since the plants die in such a solution much sooner than in distilled water.[6] A mixture of solutions which are individually poisonous produces a medium in which the plants live indefinitely.

That the plants die so quickly in solutions containing a single salt might be attributed to the fact that the osmotic pressure of some of these solutions is much lower than that of sea water. This supposition is disproved by the fact that in general the plants live longer in tap water than in any solution containing but a single salt, although the tap water has a lower osmotic pressure than that of any solution used in the experiments. (The plants of Group 1 live longer in distilled water also. The tap water is to be regarded as a physi-

[6] This statement does not apply in all cases to $CaCl_2$, which is the least toxic of the salts employed and for some forms quite harmless in dilute solutions.

ologically balanced solution; this will be more fully discussed in the second portion of the paper.)

3. The poisonous effect of NaCl is inhibited little or not at all by KCl or $MgCl_2$ added singly.

4. The combination $NaCl+KCl+CaCl_2$ is superior to $NaCl+MgCl_2+CaCl_2$, but the latter is better than $NaCl+MgCl_2+KCl$.

5. These effects must be due to the metal ions, since the anion is in nearly all cases the same.

The plants of Group 2 agree with those of Group 1 except in their behavior toward distilled water.

Essentially similar results were obtained from the study of fresh water algae and other plants, the details of which will be given in the second part of this paper.

These results agree in striking fashion with those obtained from the study of marine[7] and freshwater animals[8].

The combination $NaCl+KCl+CaCl_2$ (in the same proportions as in sea water) seems to be quite generally beneficial for animals and plants.

We may in conclusion briefly consider the effects of concentrated solutions. A series of experiments were made on *Enteromorpha Hopkirkii* in which the plants were placed in dishes with a very little sea water. This quickly evaporated, so that the plants became covered with salt crystals in 24 to 48 hours. In this condition some of them remained alive for about 150 days. This means that Enteromorpha plants which remain alive only 15 days in $3m/8$ NaCl solution can live 150 days in an NaCl solution of 10 to 12 times higher concentration, provided the other salts of the sea water are present in the solution (at corresponding concentration) to inhibit the toxic effect of NaCl. Experiments on Lyngbya, Ptilota, and Pterosiphonia gave essentially the same results.

In view of these results, and others of a similar character shortly to be published, it appears certain that physiologically balanced salt solutions have the same fundamental importance for plants as for animals.

[7] LOEB, Pflüger's Archiv **107**:252. 1905, and the literature there cited.

[8] OSTWALD, Pflüger's Archiv **106**:568. 1905. Univ. of California Publications, Physiology **2**:163. 1905.

RESULTS.

1. Each of the salts of the sea water is poisonous where it alone is present in solution.

2. In a mixture of these salts (in the proper proportions) the toxic effects are mutually counteracted. The mixture so formed is a physiologically balanced solution.

3. Such physiologically balanced solutions have the same fundamental importance for plants as for animals.

THE UNIVERSITY OF CALIFORNIA,
Berkeley.

THE APPRESSORIA OF THE ANTHRACNOSES.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXXXIV.

HEINRICH HASSELBRING.

(WITH SEVEN FIGURES)

IN describing a number of new plant diseases in 1883 FRANK[1] gave an account of peculiar spore-like organs produced by the germ tubes of spores of the bean anthracnose. He showed further that these organs acted as holdfasts, by means of which the fungus was firmly attached to its host during the early phase of development. In the same paper he described analogous organs of *Fusicladium Tremulae* and *Polystigma rubrum*. Almost simultaneously FISCH[2] described the holdfasts of Polystigma, but he did not at all recognize their true significance. He regarded them as "secondary spores" which served in the distribution of the fungus, since the ascospores are embedded in slime when ejected, and are therefore not suited for dissemination by the wind. FRANK first recognized the true nature of these bodies, and gave to all organs of this class the name *appressoria* or adhesion organs. Later MEYER[3] again described and figured the adhesion organs of Polystigma, but added no new observations. In 1886 DE BARY[4] first showed that the complex adhesion organs of Sclerotinia were produced as the result of a mechanical stimulus, but BÜSGEN[5] made the most complete study from a physiological standpoint. He showed that the germ tubes of many parasitic fungi produce adhesion organs of

[1] FRANK, B., Ueber einige neue und weniger bekannte Pflanzenkrankheiten. Ber. Deutsch, Bot. Gesells. 1:29–34, 58–63. 1883; Landw. Jahrb. 12:511–539. *pls. 3.* 1883.

[2] FISCH, C., Beitrage zur Entwickelungsgeschichte einiger Ascomyceten. Bot. Zeit. 40:851–870. *pls. 2.* 1882.

[3] MEYER, B., Untersuchungen über die Entwickelung einiger parasitischer Pilze bei saprophytischer Ernährung. Landw. Jarhb. 17:915–945. *pls. 4.* 1888.

[4] DE BARY, A., Ueber einige Sclerotinien und Sclerotinien-krankheiten. Bot. Zeit. 44:377 et seq. 1886.

[5] BÜSGEN, M., Ueber einige Eigenschaften der Keimlinge parasitischer Pilze. Bot. Zeit. 51:53. 1893.

various forms, and that their formation is due to a mechanical stimulus resulting from contact of the germ tube with some solid body.

These accounts seem to have escaped entirely the notice of American writers on the bitter rot, as is indicated by the many speculations and by the curious interpretations of the characteristic adhesion organs of the bitter-rot fungus and of other anthracnoses. The first economic account of the bitter rot appears in the *Report* of the chief of the Section of Vegetable Pathology for 1887.[6] Here the formation and germination of the appressoria are described. They are regarded as secondary spores, but no particular function is attributed to them. Excellent figures are also given on *plate 3* of the *Report* of 1890[7]. In 1891 Miss E. A. SOUTHWORTH[8] published the most complete account of the fungus up to that time. Regarding the "secondary spores" Miss SOUTHWORTH says: "What the conditions were that decided their appearance could not be determined. They were produced both in nutritive media and water, but seemed to be especially numerous where the ends of the hyphae came in contact with some hard substance like the cover-glass, and in two cases the addition of an extra drop of nutritive medium had the effect of stopping their formation." As to their function nothing is said, except that they are regarded as resting spores. (See *note*, p. 142.) In 1892 HALSTED published a short account of the secondary spores of anthracnoses.[9] He extends the list of anthracnoses which produce these organs to twenty-five species, including members of both Gloeosporium and Colletotrichum. ALWOOD[10] describes the production of "resting spores" by the bitter-rot fungus, but from his figures and description it is impossible to determine whether he had before him the bodies in question. Other writers have followed these investigators in their interpretation of the peculiar adhesion

[6] SCRIBNER, F. LAMSON, Bitter rot of apples. Rep. Sect. Vegt. Path. U. S. Dept. Agr. **1887**: 348–350.

GALLOWAY, B. T., Ripe rot of grapes and apples. *Idem.* **1890**: 408

[8] SOUTHWORTH, E. A., Ripe rot of grapes and apples. Journ. Myc. **6**: 164–173. *pl. 1.* 1891.

[9] HALSTED, B. D., The secondary spores in anthracnoses. N. J. Agr. Exp. Sta. Rep. **1892**: 303.

[10] ALWOOD, W. B., Ripe or bitter rot of apples. Agr. Exp. Sta. Va. Bull. 40. 1894.

organs of Gloeosporium. CLINTON[11] regards them as chlamydospores. They are also briefly described by VON SCHRENK and SPAULDING[12] who add *Gloeosporium cactorum* to the list of anthracnoses producing them. In order to clear up the uncertainty expressed in the literature regarding these organs, the following experiments and observations on the appressoria of *Gloeosporium fructigenum* are here recorded.

FORMATION OF APPRESSORIA.

As has been said, DE BARY and BÜSGEN have shown that the stimulus of mechanical contact is the cause of the formation of adhesion organs. Regarding the adhesion organs of Gloeosporium Miss SOUTHWORTH mentions the fact that they are especially numerous where a hypha comes into contact with some hard object like the cover glass. HALSTED finds that a rich nutrient medium produces only a meager supply of "special cells," while pure water increases their production. In neither case were these suggestions further investigated. Other writers had suggested in a general way that "unfavorable conditions" and starvation of mycelium cause the formation of the special cells.

Spores were sown in convex drops of water on slides kept in a moist chamber. Under these conditions the spores germinate rapidly, but their behavior varies according to their position in the drops. Those which sink to the bottom of the drop form a short germ tube, which enlarges into a round or pear-shaped disc when it comes into contact with the glass. In 12 to 18 hours this disc has developed into a complete adhesion organ (*fig. 1*). It is a brown spore-like body, having a thick wall which is perforated on its lower appressed surface with a very distinct germ pore. The adhesion

FIG. 1.—Appressoria formed by spores germinating in water on glass slides.

[11] CLINTON, G. P., Apple rots in Illinois. Univ. of Ill. Agr. Exp. Sta. Bull. 69. *pls. 10.* 1902.

[12] VON SCHRENK and SPAULDING, The bitter rot of apples. U. S. Dept. Agr. Bur. Plant Industry Bull. 44. *pls. 9.* 1903.

organs are so firmly fixed to the slide that they are not easily washed off by a jet of water. Other spores remain floating in the drops of water, being held by the surface film. These also germinate readily, but they never form adhesion discs while the germ tubes remain free in the water. Other spores were sown in drops of water placed on the surface of apples. These behaved in the same way as those on slides. Spores in hanging drops produced mostly mycelia, since very few germ tubes came into contact with the glass. The experiment was then varied by substituting beet infusion for the drops of water. The result was striking. The germ tubes produced no appressoria, but grew out into long hyphae, regardless of the fact that they were often in contact with the surface of the glass or with the cuticle of the apple. When sown in nutrient media of any kind, solid or liquid, the spores of Gloeosporium germinate and form mycelia directly.

These experiments show that the formation of appressoria is induced by a contact stimulus, but in the presence of abundant nutrient material the germ tube loses its power to react to contact stimuli, and the formation of appressoria is inhibited. If this were not the case, the mycelium would react to the contact of every obstacle, such as cell walls or starch grains, which it met in its course through the tissues, and growth would thus be made practically impossible. This is illustrated by the behavior of spores in weak beet infusion. Here the germ tube shows a tendency to form an appressorium, but before this is well formed it grows out again into a mycelial hypha, which immediately repeats the process. In old agar cultures which have been exhausted, the hyphae form a series of thick-walled cells of the nature of appressoria. These do not have the normal shape, but assume fantastically lobed forms, so closely crowded that they resemble sclerotia-like masses. The exhaustion of the nutrient material in the agar and the contact with the glass or other solid particles no doubt leads to the formation of these masses.

GERMINATION OF THE APPRESSORIA.

The appressoria germinate readily on a slide when covered with nutrient solution. The germ tube always emerges from the pore

on the surface appressed to the glass. By its vigorous growth it tilts the body to one side (*fig. 2*).

The process of penetration was observed by sowing spores on berries of *Berberis Thunbergii*, which are readily infected by the fungus, although some other species seem to be immune. From the pore on the lower flattened side of the adhesion disc, a slender tube protrudes and dissolves an arrow channel in the wax covering the cuticle. Although at first very slender, the hypha soon becomes larger and dissolves large cavities in the wax (*figs. 3, 4*). The fact that these cavities are more extensive than is necessary for the accommodation of the germ tube would seem to indicate that a solvent is secreted in sufficient quantities to accumulate on the outside of the infecting hypha. Finally the cell wall is perforated and the mycelium branches freely within the cells, at the same time sending hyphae into the neighboring cells. The penetration of the germ tube through the cuticle of the apple has frequently been observed, although it has not been possible to follow the mycelium farther, probably on account of the early collapse of the cells and the consequent

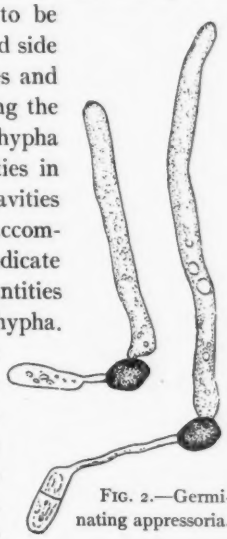

FIG. 2.—Germinating appressoria.

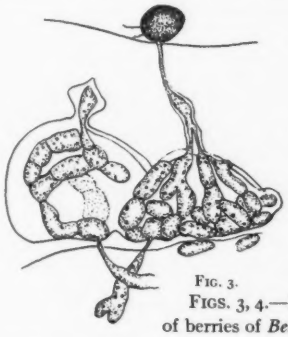

FIG. 3.

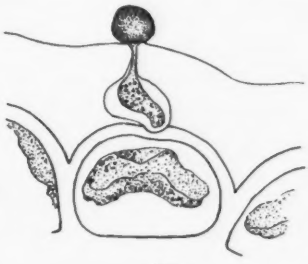

FIG. 4.

FIGS. 3, 4.—Infecting hyphae penetrating the cuticle of berries of *Berberis Thunbergii*.

accumulation of débris. The channel in this case is very narrow but well defined. Contrary to former supposition no previous injury

or puncture of the fruit is necessary. This is further demonstrated by the number of infections occurring in apples. In some cases 100 to 200 infections were found on single apples, and recently SCOTT[13] reports the enormous number of 1,000 to 1,200 infections on single fruits. It is not likely that these represent previous mechanical injury to the fruits.

APPRESSORIA IN RELATION TO DISSEMINATION.

The behavior of the appressoria of the bitter-rot fungus under natural conditions is of interest from a biological standpoint. The spores of this fungus are imbedded in a gelatinous substance, which causes them to stick together in waxy masses when dry. By reason of this condition the spores cannot be distributed by wind. So far as known they are entirely dependent for their dissemination upon rain, although it is probable that insects take an active part in carrying the spores from tree to tree. Each season the first general infection of apples by the bitter rot is due to rain washing the spores from the limb cankers, in which the fungus hibernates, to the apples below. This is plainly shown by the observation that on a tree the infected apples are distributed within an area that can be circumscribed by a cone having its apex at the canker, the source of infection. Furthermore, drops of rainwater, collected from badly infected trees, usually contain numerous spores of the bitter-rot fungus.

Since the rain, at least in many cases, is the chief factor in distributing the bitter-rot spores, it is of interest to determine the effect of wetting and drying on the spores, and also the relative vitality of the spores and the appressoria. It should be stated, that while the spores are imbedded in their mucilaginous covering, they retain their vitality for a long time, but not during the entire winter, as has often been reported. In the latitude of Southern Illinois, spores remaining on apples under the trees either germinate[14] or perish long before spring. Spores taken from time to time from a diseased apple, which was kept dry in the laboratory from August until January, showed a large percentage of germination as late as Nov. 29, but later rapidly lost their vitality.

[13] SCOTT, W. M., The control of apple bitter rot. U. S. Dept. Agr. Bur. Pl. Industry Bull. 93. *pls.* 8. 1906.

[14] See also CLINTON, *l. c.*

To test the resistance of spores to drying after being freed from the surrounding mucilage by washing, a quantity of spores was shaken up with water and then spread out on glass slides which were allowed to dry. After remaining dry 14 hours, few spores germinated when again placed in water; after 24 hours, none germinated. At different times during the summer spores were shaken up in water and sprayed on filter paper, apples, and glass slides, but it was impossible to cause them to germinate after having been dried 24–30 hours.

That the appressoria are more resistant is shown by the following experiment. Appressoria were produced by sowing spores in drops of water on slides which were kept in a moist chamber until the following day. The slides were then allowed to dry, all the submerged spores having produced appressoria. The germination of the appressoria was tested from time to time by covering a slide with sugar-beet infusion. The appressoria germinated, though irregularly, as late as Dec. 11, when the last slide was used.

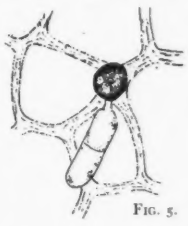

FIG. 5.

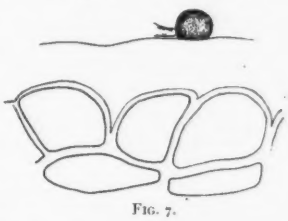

FIG. 7.

FIGS. 5, 6.—Natural appressoria formed on the surface of apples.

FIG. 7.—Section showing relation of adhesion organ to cuticle of apple.

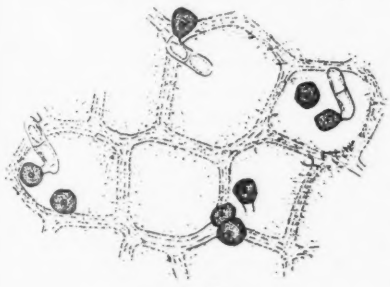

FIG. 6.

During the hot summer weather the bitter-rot spores germinate immediately, and in 12–24 hours the appressoria are formed. Under natural conditions the germ tube is extremely short, since it immediately proceeds to the formation of an adhesion-disc. From this firmly adherent and more resistant organ the infecting hypha dissolves its way into the fruit. In badly infected trees the appressoria can often be found in great numbers adhering to the surface of the

apples. Such naturally formed appressoria are shown in *figs. 5, 6*, while in *fig. 7* a single adhesion organ is shown in section.

CONCLUSIONS.

The spore-like organs formed by the germ tubes of the anthracnoses are adhesion organs, by means of which the fungus is attached to the surface of its host during the early stages of infection. They are not suited for dissemination and therefore are not to be regarded as spores. The adhesion discs are formed as a result of stimuli from mechanical contact acting on the germ tubes. When growing in nutrient media the germ tubes lose their power of reacting to contact stimuli by the formation of appressoria. Under natural conditions the appressoria are formed as soon as the germ tube emerges from the spore.

NOTE.—In the same year ATKINSON describes these bodies for a species of Colletotrichum (*C. Gossypii*)[15] and suggests that their production in unfavorable conditions seems to favor the notion that they are resting bodies.

[15] ATKINSON, G. F., Anthracnoses of cotton. Journ. Mycol. **6**:173–8. *pls. 2.* 1891.

THE UNIVERSITY OF CHICAGO.

BRIEFER ARTICLES.

NEREOCYSTIS LUETKEANA.

(WITH ONE FIGURE)

This giant kelp is one of the most common, and certainly one of the most striking algae of the shores of northwest America. Its cylindrical, hollow stalks, as much as 21^m long, gradually widening from a diameter of 1^{cm} below to 10^{cm} above, surmounted by a bulb as much as 20^{cm} in diameter and provided with a crown of leaf-like fronds $3–9^m$ long; its habitat on submerged rocks over which it forms brown patches acres in extent, a warning to fishermen and pilots, and so dense that only with great difficulty can one get a rowboat through them; its presence everywhere in still waters and stranded along shores, torn loose and transported by waves and wind, attract the attention of every casual traveler along north Pacific shores. Two things concerning this plant at once impress the botanist, viz.: its remarkably rapid growth and its manner of solving the problems of life.

1. *Growth.*—We have here a plant $15–21^m$ long,[1] reported to reach a length of over 90^m,[2] but probably erroneously; MACMILLAN[3] mentions 80 feet. HARVEY[4] states that it is growing at all seasons; fishermen and pilots, however, say that it disappears in winter. I knew the June condition of these plants, and I had accurately located several beds of them near the Marine Station of the University of Washington at Friday Harbor, Wash., during the summers of 1904 and 1905. On March 10, 1906, I made another trip to these beds with a view to determining whether or not this gigantic plant is an annual. The fishermen are partly right. Except for stragglers here and there, the kelps are gone; while those remaining were nearly all decayed and loose, with their fronds mostly torn away. Where the plants were floating freely, the remaining ones were yet in fair condition as to decay, as salt water prevents rapid bacterial action; but it required considerable searching to find a dozen good specimens.

Drifting over the reefs one can see, through a glass-bottomed bucket, on the bottom 3 to 9^m below, young plants of Nereocystis 1.25 to 2.5^m

[1] SAUNDERS, Algae of Harriman Alaska Expedition. Proc. Wash. Acad. Sci. **3**:431.

[2] ENGLER & PRANTL, Die natürlichen Pflanzenfamilien 1^2:259.

[3] Bull. Torr. Bot. Club **26**:273–299. 1899.

[4] Sea mosses 87.

long, with bulbs 12 to 38^{mm} in diameter, and fronds 30 to 90^{cm} long. It seems that they do not reach the surface the first year, but remain out of reach of waves, pushing rapidly up in the second season only to die when winter overtakes them. A growth of about 18^{m} in the second year, between the middle of March and the first of June, a period of about 70 days, requires on the average a growth of over 25^{cm} a day. The probability is that it is even greater, for March is cool on Puget Sound, so the growth would occur chiefly in the latter part of this period. In proof of this

FIG. 1.—*Nereocystis Luetkeana.*

belief is the fact that the ground was frozen during the whole week succeeding the time of observation; in fact, it was the coldest weather of the whole winter. Then too, another trip on May 10, 1906, but to a different bed, revealed none over 6^{m} long; so it is evident that they had 9 to 15^{m} of stretching before them for the next month. Twenty-five centimeters per day is about 0.175^{mm} per minute, which is between one-third and one-fourth as rapid as that reported for the bamboo,[5] and far above that of ordinary plants. One hardly expects prolonged rapid growth in the latitude of Puget Sound, but Nereocystis certainly furnishes an example of it.

[5] STRASBURGER *et. al.*, A text book of botany, English edition, 231. 1903.

2. *Life relation.*—The shore just below low tide to a depth of 6^m is taken up by shorter, broad algae, mostly brown, many green, a few red; limited up shore by the grinding wave-washed rocks as the tide level varies, and by the baking heat of a summer sun during low spring-tides; limited downwards by the decreasing sunlight; we find on this strip the battle ground of the green and brown algae, species against species. Nereocystis, with its tough, flexible, cattle-whip-like stalk 12 to 21^m long, rises from the bottom in the deeper waters, a veritable Esau, surrendering to the Jacobs the coveted strip and wresting from the undesired, comparatively unoccupied territory beyond, a highly successful existence. The stalk is firmly anchored to the rocks below by holdfasts covering an area as much as 30^{cm} in diameter. So strong and tough is the stalk, and so firm the attachment, that often a pull of several hundred pounds is necessary to loosen the plant; and then the stalk more often than the holdfast gives way; but a large plant, avoiding quiet waters, needs a firm hold, and one occasionally finds the plants washed ashore with holdfasts dragging rocks as much as 20^{cm} in diameter. The admonition to "build upon a rock" holds for Nereocystis, and the rock must be a big one; those which "build upon sand" are washed away before they reach the adult stage. This is one of the reasons why it grows upon reefs.

Algae love moving water, but few can afford it. Moving water facilitates gas exchange by carrying away that ladened with evolved and lacking in desired gases, and by not depositing suspended materials like quiet water. A layer of beach washings over a plant absorbs sunlight, one of the scarcer commodities of marine algae, any diminution of which only those most favorably located can afford. Nereocystis, by its firm anchorage and long stalks, surmounted by a bunch of tough blades 3 to 9^m long but narrow for their length, rides easily in flowing water, and chooses for its home the rocky, clean-swept, tide-washed promontories, where the current keeps its blades horizontal.

Below 6^m the brown algae rapidly decrease, and dredging in Puget Sound shows that below 12^m they are exceptional. They need light. It is well known too, that the decrease in light downward in water is rapid. This makes the surface the most desirable location. But shore forms, at the surface at high tide, are stranded high and dry at low tide; and those at the surface at low tide are covered at high tide, the depth depending upon the difference between high and low tide. This constant change in water level is one of the greatest difficulties with which seaweeds have to contend. We see at once that marine algae have a very serious problem, to steer clear of the Scylla of darkness on the one hand, and, on the other,

at a very short bow-shot's distance, the Charybdis of tide-line destruction by wave and sun. Nereocystis has solved the problem by the floating dock. Its holdfast at the smaller end of the stalk serves as the anchor, fastened far enough off shore to prevent stranding at low tide; its hollow bulb, surmounting the larger, hollow end of the stalk is the float; attached to the bulb are the leaves, constantly at the surface, supple, tough, safe in storm, current, and varying tide. However, it has minor troubles, since in creating for its own fronds an excellent environment it has created also an excellent habitat for other forms as well. It is not uncommon to see the bulbs and stalks densely covered with delicate red and green algae, and hydroids and bryozoa. Rising from unoccupied territory, and creating for its fronds one of the best habitats among marine algae, *Nereocystis Luetkeana* challenges the respect of the botanist and the lover of nature.—THEODORE C. FRYE, *State University, Seattle, Washington.*

TWO NEW SPECIES FROM NORTHWESTERN AMERICA.

MISS EDITH M. FARR of Philadelphia has recently submitted to the writer a small collection of plants for identification. The collection was made in the mountainous regions of Alberta and British Columbia, chiefly in the vicinity of Banff, Lake Louise, Field, etc., during the summers of 1904 and 1905. Among other interesting rarities there are two which the writer has been unable to place satisfactorily in any described species. These are characterized as follows:

Castilleja purpurascens Greenman, n. sp.—Perennial, more or less purplish throughout: stems erect or nearly so, 1 to 3^{dm} high, usually several from a multicipital caudex, glabrous or puberulent below, villous above: leaves sessile, subamplexicaul, linear to narrowly lanceolate, 1.5 to 4.5^{cm} long, 1 to 7^{mm} broad, usually attenuate and acute, entire and undivided or occasionally 3-cleft near the apex, glabrous or the upper somewhat villous-pubescent, 3-nerved; the lowermost leaves much reduced: inflorescence terminating the stem in a subcapitate raceme, later elongating to about 7^{cm} in length, villous-pubescent; bracts ovate-lanceolate to oblong-ovate, 2 to 2.5^{cm} long, usually entire, occasionally cleft: calyx 1.5 to 2.5^{cm} long, and as well as the bracts varying in color from a deep purplish-red to scarlet and rarely to yellow tinged with red or pink, about equally divided before and behind, externally villous with glandular hairs intermixed; the lateral divisions 2-lobed, lobes obtuse: corolla 2 to 3^{cm} long; galea about one-half as long as the corolla-tube, green or greenish-yellow on the glandular puberulent back, with scarlet or magenta colored

margins, conspicuously exserted beyond the calyx and floral bracts; lip usually dark green, 3-lobed, about one-fourth the length of the galea, commonly protruding through the anterior fissure of the calyx: mature capsule oblong, 7 to 8^{mm} long, abruptly acuminate or subapiculate, strongly compressed laterally, glabrous: seeds about 1.5^{mm} long, yellowish-brown.

BRITISH COLUMBIA: near Field, at an altitude of about 1200^{m}, 7 June, 1905, Miss *Edith M. Farr*, nos. 567, 568 (type), 569, 570, 571, 572, 573, 574 (form with yellowish inflorescence slightly tinged with red or pink), 575, 576. Type in hb. Field Museum and hb. Univ. of Penn.

The suite of specimens here cited shows considerable variation in color and to some extent variation in foliage, but all have the same habit and technical characters of the flower. The species apparently has its nearest affinity with *Castilleja Elmeri* Fernald, from which it differs in being glabrous or essentially so below, in having a more slender inflorescence, narrower floral bracts, and a more conspicuously exserted corolla with a somewhat longer galea. The purplish cast of the entire plant with the galea extending well beyond the crimson or purplish bracts and calyx renders this an attractive species and easily distinguished among its numerous allies.

Senecio (§AUREI) **Farriae** Greenman, n. sp.—An herbaceous perennial 1 to 1.5^{dm} high: stem erect or ascending, branching from near the base, glabrous except for a persistent white tomentum in the leaf axils; branches few, relatively long and terminated by a single head: basal leaves ovate to slightly obovate, the blade 1 to 3^{cm} long, 1 to 1.5^{cm} broad, rounded at the apex, crenate-serrate to subentire, contracted at the base into a narrowly winged petiole equaling or exceeding the blade, glabrous or nearly so; the lower stem leaves sublyrate or more or less irregularly pinnatifid, the upper reduced to entire bracts: heads about 1^{cm} high, radiate: involucre campanulate, slightly calyculate, tomentulose at the base; bracts of the involucre usually 21, linear-lanceolate, about 8^{mm} long, nearly or quite equaling the flowers of the disk, acute, reddish tipped: ray-flowers 12 to 14; rays orange-yellow; disk-flowers numerous.

ALBERTA: near Banff, altitude 1500^{m}, 8 June, 1904, Miss *Edith M. Farr*. Type in hb. Univ. of Penn., fragment and photograph in hb. Field Museum.—J. M. GREENMAN, *Field Museum of Natural History, Chicago.*

CURRENT LITERATURE.

BOOK REVIEWS.

Plant response.

No SUBJECT is more fascinating than the responses of plants to stimuli; and though the mechanisms involved are often much simpler than in the case of animals, no subject is more difficult. Papers dealing with limited topics in this field are constantly appearing; one feels some surprise at seeing a large volume of new researches dealing with the matter in the most fundamental fashion. The surprise is increased when it is seen that the author is one whose name is new in the literature of plant physiology and whose nation is fond rather of speculative philosophy than of scientific observation. Professor JAGADIS CHUNDER BOSE of Presidency College, Calcutta, published in 1902 a volume on *Response in the living and non-living*, in which he pointed out many parallels between the "irritability" of organisms and of other bodies. But this volume seems not to have attracted general attention among physiologists; and some of those who read it were inclined to discount the parallelism as one suggested rather by philosophic bias than scientific induction.

On opening this new work[1] the plant physiologist will be inclined to think it some volume on muscle-response in animals, the numerous graphs being quite like those made familiar by the usual records from muscle-nerve apparatus. Closer inspection, however, shows that the author, trained in a laboratory for animal physiology and in the methods of research in vogue for pulse and muscle, has applied these methods to detecting before unsuspected (or at least unrecorded) responses in plants.

But he has done much more than merely apply the existing apparatus and methods. He has employed new methods and has devised new and ingenious apparatus for automatically recording responses. For example, there are described many clever minor adaptations of the optic lever and various electric devices; and among the major ones may be enumerated the kunchangraph (Sanskrit: *kunchan*=contraction) for recording longitudinal contraction in radial organs on applying electric, thermic, or chemic stimuli; the morograph, for recording the death spasm of the contractile protoplasm, and the comparison morograph for recording the response of two plants simultaneously while under different conditions; the shoshungraph (Sanskrit: *shoshun*=suction) for recording the rate of transpiratory suction and its variations; the crescograph,

[1] BOSE, J. G., Plant response as a means of physiological investigation. 8vo. pp. 781. *figs.* 278. London, New York, and Bombay: Longmans, Green, & Co. 1906.

balanced so as to record the average rate of growth as a straight horizontal line, any fluctuation, even the slightest, showing as deviation from this horizontal line; and the magnetically controlled heliotropic recorder, utilizing the optic lever yet avoiding the use of light within the plant chamber, except that which is the stimulus.

One striking feature of all the apparatus, aside from its ingenuity, is the high magnification which it permits. This is at once an advantage and a danger; but consistent results, if critically controlled, ought to guard against serious error.

The book is not without errors, both of reasoning and fact, into which the author has fallen by reason of some unfamiliarity with his materials. No one could justify himself in accepting as established all the deductions from the vast number of experiments detailed in the book; they must be verified sooner or later by other observers. To our knowledge some have already been repeated (some of those, for instance, on the variation in electric potential resulting from stimulation, in Dr. HARPER'S laboratory at the University of Wisconsin) with concordant results. But whatever the future may show as to the accuracy of details, this book may be acclaimed as a path-breaking one; for it shows a method of attack and a refinement of instrumentation for the study of the phenomena of irritable reactions in plants that are sure to be of the utmost service. It is rather remarkable, indeed, that we have had so few recording instruments in the service of plant physiology, and that we have been content, for example, with magnifications of 10 or 20 times in the auxanometer, where BOSE finds 1,000 or even 10,000 practicable with his crescograph.

The fundamental thesis of the book is that the underlying response to stimuli is alike in plants and animals; is alike in all plants and in all parts, with all stimuli; and is universal. This response, however diverse its modes of expression, consists of two very simple and well-defined factors, contraction and expansion; the former the direct effect of stimulation, the latter the indirect. Mechanical response is always by a concavity of the more excited side and may or may not occur; electrical response can always be detected; growth is merely a multiple response; at death (near 60° C. for phanerogams) a sudden and irreversible molecular change takes place, attended by an excitatory contraction. The phenomena of fatigue, of staircase response when the organ is at first sluggish, of tetanus, of the polar effects of electric currents, of variation in electric potential, of transmission of stimuli, and of rhythmic responses—all can be demonstrated in plants as in animals, giving evidence in greater detail of the essential unity. With this BOSE is more impressed and on it he lays more stress than the case demands; for it is by no means so novel an idea to botanists as to most zoologists.

Of all the fifty chapters in the book none are so unsatisfactory as those on the ascent of sap, constituting part V. BOSE holds that he has demonstrated the ascent of water to be due to the physiological activity of living cells whose suctional response is coordinated by the passage from point to point of an exci-

tatory reaction which drives water in one direction.[2] But some of his reasoning is radically defective, the chapters are full of assumptions, and his experiments are inconclusive. Indeed, he hardly seems to know how difficult a problem he is attacking, and he goes at it with the naïveté of a novice. Such work really tends to prejudice one against the whole book; and caution *is* necessary, for there are other weak spots. In spite of these, the suggestiveness, the ingenuity, and the enormous labor displayed impel us to give this book a most cordial reception. And we shall await with much interest a promised volume on the electrophysiology of plants.—C. R. B.

MINOR NOTICES.

N. Am. Uredineae.—The second part of HOLWAY's photomicrographs of plant rusts[3] has just appeared, having been delayed several months by a printer's strike. The general character and purpose of this publication were described in this journal[4] upon the appearance of the first part. The present part continues the genus Puccinia through eleven host families, ending with Rosaceae. The photogravure plates carry out fully the promise of the first part.—J. M. C.

Schneider's Handbuch.—The fifth part of the *Illustriertes Handbuch der Laubholzkunde*[5] concludes Drupaceae and includes Pomaceae, and ends the first volume. There are 128 text figures, and a volume index of genera.—J. M. C.

NOTES FOR STUDENTS.

The ascent of water.—After GODLEWSKI's interesting theory of the relay-pump action of the medullary rays in lifting water seemed to have been completely overthrown by STRASBURGER,[6] who found water still ascending for weeks after treatment calculated to kill living cells, the participation of living cells in lifting water found a champion on theoretical grounds in SCHWENDENER.[7] But PFEFFER[8] hardly dared more than to suggest that they might be of importance in

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[2] See in this connection reviews of other recent papers below.

[3] HOLWAY, E. W. D., North American Uredineae, Vol. I. part II. 4to. pp. 33–56. *pls. 11–23.* Minneapolis, 1906. $2.00.

[4] BOT. GAZETTE **40**:459. 1905.

[5] SCHNEIDER, CAMILLO KARL, Illustriertes Handbuch der Laubholzkunde. Fünfte Lieferung. Jena: Gustav Fischer. 1906. *M* 4.

[6] STRASBURGER, E., Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Histologische Beiträge **3**. Jena, 1891. Ueber das Saftsteigen. Histologische Beiträge **5**. Jena, 1893.

[7] SCHWENDENER, S., Zur Kritik der neuesten Untersuchungen über das Saftsteigen. Sitzb. Berliner Akad. **44**:911–946. 1892. Gesammelte Unters. **1**:256–297. Weitere Ausführungen über die durch Saugung bewirkte Wasserbewegung in der Jamin'schen Ketten. Sitzb. Berliner Akad. **45**:835–846. 1893. Gesammelte Unters. **1**:298–315. 1898.

[8] PFEFFER, W., Pflanzenphysiologie **1**:203. 1897.

the maintenance of normal conditions in the conducting tissues. Then URSPRUNG rallied to the support of SCHWENDENER with experimental work, and in a paper published two years ago[9] contended that the living cells, either by maintaining the conducting system in condition or by actually lifting, had an important share in the ascent of water. His experiments were carried out on small plants mainly, and he ventured no generalization.

In a more recent paper[10] he reviews critically the direct and incidental experiments of others on this subject, replies to objections raised against his earlier paper; and details further experiments intended to ascertain the precise rôle of living cells. The author adopts a rather hypercritical attitude toward previous results, as is well illustrated by this reasoning regarding girdling: "If at the base girdling 1^{dm} long is borne without injury, it does not signify that this would be the case also at the apex; and if girdling 1^{dm} long does not interrupt the conduction of water, it is not proved that this would not occur with girdling one or two meters long. Hence it follows that the bark (*Rinde*) must be entirely removed if one wishes to form a judgment as to its share in the ascent of sap; and even then one can at most only recognize that it may be dispensed with—not that under ordinary conditions it takes no part in the ascent of sap."

By liberal discounts URSPRUNG arrives at the conclusion that *all* previous researches on this point speak in favor of the participation of living cells in raising water. Even the experiments of STRASBURGER, which have been interpreted as flatly contradictory to such an idea, are counted as offset by his finding that the leaves die after one actually kills 10^{cm} of the stem. For, according to URSPRUNG, the cooperation of living cells throughout the entire length of the plant is necessary; but a small fraction of the conducting system suffices to supply water if in this region the wood cells are living; whereas the whole is inadequate to furnish enough water when they are killed. These living cells do not merely keep the conducting tissues in good condition; they "cooperate in the production of the lifting force," and the component which they furnish is of great significance in comparison with the "purely physical." A notable exception is the beech, in whose older parts the cells of the bark are without influence, "and even in the youngest parts such interaction is insignificant." It is hard to conceive how the living cells in the bark, being outside the water paths, can participate in the work of raising water, and harder still to imagine that they do so in certain plants and not in others.

STEINBRINCK attacks the problem from the "purely physical" side,[11] and

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[9] URSPRUNG, A., Untersuchungen über die Beteiligung lebender Zellen am Saftsteigen. Beihefte Bot. Cent. **18**:145–158. 1904.

[10] ———————, Die Beteiligung lebender Zellen am Saftsteigen. Jahrb. Wiss. Bot. **42**:503–544. 1906.

[11] STEINBRINCK, C. Untersuchung über die Kohäsion strömender Flussigkeiten mit Beziehung auf das Saftsteigeproblem der Bäume. Jahrb. Wiss. Bot. **42**:579–625. 1906.

seeks to extend our knowledge of hydrodynamics. He examined the cohesion of water by means of the supersiphon, i. e., a siphon whose legs are so long as to permit the use of columns of liquid too high to be raised by atmospheric pressure, to which (STEINBRINCK thinks erroneously[12]) the action of the common siphon is ascribed. He attempted to ascertain the cohesion of water under various conditions, and met sometimes with such capricious behavior of his apparatus that, more than ever by this experience, he is convinced of the necessity for much more extended physical knowledge before the problem of the ascent of sap can be solved. The reinvestigation of the tension of gases in fern and other sporangia (which he finds nearly at atmospheric pressure) and of their disappearance when the sporangia are wetted, shows that these phenomena do not fall in with any known physical laws; and as these structures plainly contain only dead cells the problem cannot be obscured by dragging in "vital activities" and remains at present inexplicable. How much more caution, then, is needed in the more complex problem of sap movement!

STEINBRINCK finds that a water filament 2^{mm} thick, moving at the rate of 2^{cm} per second, bears a pull of four atmospheres, its tensile strength increasing with diminishing size and rate of flow. Such filaments bear even violent shaking, under certain conditions, without rupture. Their stability is not affected by extremes of temperature that would be encountered in the growing season (say 0° to 35° C.). By ingenious experiments he shows that cohesion may act through membranes, such as the partitions that interrupt the tracheae. As for the objection to the cohesion theory on account of the Jamin-chain condition, he suggests caution on account of deficient physical knowledge, enforcing this by citing the case of gas absorption in the opening sporangia already alluded to. He does not deny the participation of living cells, but can form no conception of the manner in which they act.

EWART, recognizing that water is a liquid of definite viscosity and that the channels through which it moves are small, thereby offering great resistance, has endeavored to ascertain the amount of this resistance in definite cases, and the possible means by which is generated the force necessary to raise water at the required rate.[13] He finds that the flow of water through open vessels is in accord with POISEUILLE'S formula deduced from flow through rigid tubes; hence the velocity is proportional to the pressure and to the square of the radius of the tube, and inversely proportional to the length of tube and viscosity of the liquid. The total resistance in erect stems corresponds to a head of water 6 to 33 (for shrubs and small trees) or 5 to 7 (for large trees) times the height of the plant. Hence, in the tallest trees, the pressure required may be as much as 100 atmospheres. The maximal osmotic suction of leaves in an elm 18^{m} high was 2–3

[12] STEINBRINCK, C. Ueber dynamische Wirkung innere Spannungsdifferenzen etc. Flora **93**:127–254. 1904.

[13] EWART, A. J., The ascent of water in trees. Phil. Trans. Roy. Soc. London B. **198**:41–85. 1905.

atmospheres, with a total resistance to flow in the trunk of 10–12A. "It appears, therefore," concludes EWART, "that to maintain flow, a pumping action of some kind or other must be exercised in the wood, for which the presence of active living cells is essential. . . . . There is no known means by which these cells can directly pump water in a definite direction. . . . . It is suggested that the wood parenchyma cells, by the excretion and reabsorption of dissolved materials, may bring into play surface tension forces within the vessels of sufficient aggregate intensity to maintain a steady upward flow, and to keep the water of the Jamin's chains in the vessel in a mobile condition, ready to flow to wherever suction is exercised."

But STEINBRINCK declares himself (*l. c.*) unable to form any conception of how such an action can be produced, and LARMOR objects[14] on purely mechanical grounds, saying: "If the osmotic gradient, assisted by capillary pull at the leaf orifices, is insufficient to direct a current of transpiration upward, *capillary* alterations inside the vessels, arising from vitally controlled emission and absorption of material from the walls cannot be invoked to assist." He suggests that *osmotic* changes in the vessels, of peristaltic character, might do; but he apparently does not know that osmotic phenomena do not occur in sap vessels. As a physicist, he inquires whether there is a sufficient stock of energy in the stems for the pumping work required; and he renews the eminently plausible suggestion that the work is done where the external energy is received, viz., in the leaves.

It cannot be said that these researches have solved the problem of water movement. But each in its own way has added something to our knowledge. The more hopeful lines seem to be in determining physical factors and studying more closely the dynamics of the question.—C. R. B.

Gymnosporangium galls.—The anatomical changes induced by *Gymnosporangium clavariaeforme* and *G. juniperinum* on the twigs and leaves of their host, *Juniperus communis*, have been investigated by LAMARLIÈRE[15] with the following main results. The mycelium of *G. clavariaeforme* inhabits the cortex and phloem regions, but does not penetrate into the wood. The cells of the cortex are multiplied and enlarged so that all lacunae are obliterated, resulting in a general hypertrophy of this region. The formation of collenchymatous tissue is almost entirely suppressed. In the phloem region the medullary rays undergo the most marked transformation. Not only do the rays themselves become more numerous, but the cells composing them are also greatly increased in number, so that this tissue is likely to make up about one-half the volume of the bast region. The sieve tubes, parenchyma, and bast fibers retain their normal succession, but owing to the great increase in parenchyma from the rays and from the increased volume of the bast parenchyma, the course of the sieve

[14] LARMOR, J., Note on the mechanics of the ascent of sap in trees. Proc. Roy. Soc. B. **76**:460–3. 1905.

[15] LAMARLIÈRE, L. GÉNEAU DE, Sur les mycocécidies des Gymnosporangium. Ann. Sc. Nat. Bot. IX. **2**:313–350. *pls. 8–12.* 1905.

tubes and bast fibers becomes distorted and irregular. The cambium ring also is broken and irregular from the fact that uniform differentiation into phloem and xylem no longer occurs. In the wood the medullary rays undergo transformation as in the phloem, becoming irregular masses of parenchymatous storage tissue. The wood is also considerably enlarged.

In *G. juniperinum* the changes are similar but less marked, the greatest changes in the medullary rays being near the periphery. The sieve tubes are mostly suppressed and the xylem is somewhat reduced. In the leaves the chief change induced by this fungus is the transformation of the spongy parenchyma into palisade-like tissue. The observations of this writer agree in detail with the more extensive account of WOERNLE, whose excellent paper on the anatomical changes induced by both the European and American species of Gymnosporangium is nowhere cited or referred to in the article.

As a general result of the effects of the fungus on its host, LAMARLIÈRE points out the tendency toward "parenchymatization," i. e., a tendency of the cells to remain in their more undifferentiated form, a phenomenon from which he draws a parallel to tuber formation.—H. HASSELBRING.

Dioecism among Mucorales.—In continuation of his studies of dioecism among the Mucorales, BLAKESLEE[16] has recently investigated the extent to which differentiation of sex occurs in the spores from germ-sporangia obtained from zygospores. The principal results contained in the paper are as follows. The germ-sporangia of the homothallic species *Sporodinia grandis* and *Mucor* I (undescribed) contain but a single kind of spores, which produce mycelia again capable of forming zygospores. With the heterothallic species the case is different. Here spores in the germ-sporangium may be either all (+) or all (−), or (+) and (−) may be mixed. Of the species tested, *Mucor mucedo* produces all (+) or all (−) spores in its germ-sporangia, showing that a segregation of sex takes place at some period previous to the formation of spores. In *Phycomyces nitens*, however, (+) and (−) spores are mixed in the same germ-sporangium, together with others that show a tendency to produce a homothallic strain. The mycelia of the homothallic strain are characterized by the production of irregular contorted growths to which the writer gives the name *pseudophores*. The production of sporangia on these mycelia is very limited. The spores from them show a segregation into (+) and (−), and others reproducing the homothallic strain.

The reading of this paper is made somewhat difficult partly through lack of clearness in style, which is as essential in scientific exposition as is accuracy in investigation, and partly through the loose use of terms introduced by the author himself. The terms heterothallic and homothallic as used in the earlier papers on zygospore-formation apply to the condition of sexual differentiation of the individuals within a species, strain, or form, being equivalent to dioecious and monoecious. While it is possible to speak of a heterothallic species or race, it

[16] BLAKESLEE, A. F., Zygospore germinations in the Mucorineae. Annales Mycol. 4: 1–28. 1906.

is difficult to see how this conception can be applied to individual mycelia or to spores, or even to the process of germination, as is done repeatedly by the author. Perhaps the introduction of new terms is superfluous in this case, for the idea is well expressed by the older terms dioecious and monoecious. These are used in reference to algae, where the condition thus designated exists.—H. HASSELBRING.

Fixation of nitrogen.—The Agricultural Research Association, a Scottish society which has its station at Glasterberry near Aberdeen, has published in its Report for 1905 a paper by the Director of Research, THOMAS JAMIESON,[17] Chev. Fr., F. I. C., which is supposed to overthrow the current knowledge as to the fixation of nitrogen by the root tubercle organisms and to prove that plants of many sorts utilize the nitrogen of the air directly by means of the hairs with which the leaves are furnished. The laudations with which this pretended "research" was received at the annual meeting by men even more ignorant of the subject than the "director of research," are really worthy of a place in comic literature, were it not for its serious side in giving local currency at least to foolish notions.

The "research" itself is its own condemnation, and shows the "director" to be as ignorant of chemistry as of the physiology and anatomy of plants. Here is a serious society in Scotland, spending money for that which is not bread, lauding an imposture as a wonderful discovery, publishing a report with twelve colored plates illustrating the "albumen generators" imagined by a man who does not know the difference between surface hairs and the spiral tracheae of "Holly laurifolia"! Further it summarizes the previous "leading results" of this same "director;" among which we note the discovery that there is "an aperture in root hairs by which the absorption of insoluble matter is explained;" and that the "feathery structures in the flowers of cereals and grasses are not essential parts of the pistil but serve to drive out the anthers to the air"!

Yet we can hardly bring a railing accusation against the misled members of this society when our own postoffice department has had recently to deny the use of the mails, to prevent our own people from being swindled, to a rascal who is advertising "vineless potatoes," that produce a large crop of tubers when planted in wet sawdust and watered with "potatine" at $4.50 per! Truly, some botanical training might save the farmer from his foolish as well as his knavish friends.—C. R. B.

Corky cell-layers in monocotyledons.—MÜLLER describes[18] in detail the cutinized membranes in the root and stem of *Convallaria majalis*, viz., epiblem covering the root-cap, intercutis of greater or less thickness in the cortex of root

[17] JAMIESON, THOMAS, Report for 1905 to Agricultural Research Association. 8vo. pp. 81. 1905.

[18] MÜLLER, HEINRICH, Ueber die Metacutisierung der Wurzelspitze und über die verkorkten Scheiden in den Aehren der Monocotyledonen. Bot. Zeit. **64**:53–84. *pl. 3.* 1906.

and rhizome, endodermis, and epidermis. The microchemical reactions for each of these layers are given. A process called "metacutinization" is described, which involves all the outer cells of a root-tip, and occurs at the end of the growing season. Four stages in the development of the endodermis are distinguished, following KROEMER, viz., embryonic, primary (characterized by presence of CASPARY'S points), secondary, and tertiary (showing suberization and lignification of a large part of the wall). The endodermis of the root does not usually pass through more than the first two stages. The writer brings together the information available concerning the presence or absence of an endodermis in monocotyledonous stems, and a survey of the tables shows that in about 60 per cent of the species an endodermis is present in the underground stem, while only in Medeola and Scindapsis has an endodermis been reported for the aerial stem. The relation of the starch sheath of aerial stems to the endodermis of rhizomes was also studied, and the writer failed to establish an actual continuity between the two layers. The function of the endodermis is said to be the transfer of water and food between the central cylinder and the cortex, and the increasing cutinization is associated with the necessity for checking the movement of solutes in the radial direction.—M. A. CHRYSLER.

Items of taxonomic interest.—H. D. HOUSE (Muhlenbergia 1:127–131. 1906) publishes several changes in the nomenclature of Orchidaceae, and describes a new Californian species of Dichondra.—A. A. HELLER (*idem* 134) publishes a new Californian species of Ribes.—Under the editorship of IGN. URBAN (Engler's Bot. Jahrb. **37**:373–462. *pl. 9.* 1906) a fascicle of 18 contributions describing new Andean plants has been published, among which the following new genera appear: *Orchidotypus* (Orchidaceae), by F. KRÄNZLIN; *Laccopetalum* (Ranunculaceae), by E. ULBRICH; *Belonanthus* and *Stangea* (Valerianaceae), by P. GRAEBNER, who gives a general synopsis of the family.—R. PILGER (idem, Beiblatt 85, pp. 58–67) describes a new genus (*Lamprothyrsus*) of South American grasses near Danthonia.—S. LEM. MOORE (Jour. Botany **44**:145–154. 1906) has described 2 new genera from Madagascar: *Cloiselia* (Compositae) and *Stenandriopsis* (Acanthaceae).—R. M. HARPER (Bull. Torr. Bot. Club **33**:229–245. 1906) has described new species from the coastal plain of Georgia under Sporobolus and Nymphaea.—W. H. BLANCHARD (Rhodora **8**:95–98. 1906) has described two new species of Rubus from New England, both of them high blackberries.—A. ZAHLBRUCKNER (Ber. Deutsch. Bot. Gesell. **24**:141–146. *pl. 10.* 1906) has described a new genus (*Lindauopsis*) of parasites in the hymenium of lichens.—R. SCHLECHTER (Bot. Jahrb. **39**:161–274. *figs.* 13–23. 1906), in completing his account of New Caledonian plants, describes the following new genera: *Menepetalum* (Celastraceae), *Acropogon* (Sterculiaceae), *Memecylantus* and *Pachydiscus* (Caprifoliaceae).—J. M. C.

Double fertilization in Carpinus.—In 1893 Miss BENSON published her first paper on the embryology of the Amentiferae. This is now followed by a second

paper,[19] dealing especially with the behavior of the pollen tube in connection with double fertilization in *Carpinus Betula*. As the previous paper pointed out, this form is chalazogamic, and usually has several embryo sacs, which develop caeca that penetrate deeply into the chalazal region. The course of the pollen tube varies considerably, but usually it enters the embryo sac at the base of the caecum. Premature arrival of a pollen tube results in more or less branching and coiling about the sacs; and belated pollen tubes also occur, long after fertilization has been accomplished. The polar fusion nucleus is in the caecum, and as the pollen tube passes it one of the male cells (probably the one farthest from the tip) is discharged through a small spur-branch, the other one being discharged upon the arrival of the tip in proximity to the egg. Sometimes the spur-branch, containing a male cell, develops sufficiently to discharge it for the fertilization of the egg of an adjacent embryo sac, in this case triple fusion not occurring. The paper also presents a somewhat elaborate comparison of Carpinus and Casuarina, as the basis of a suggestion that the latter genus should be regarded as a subfamily of Betulaceae.—J. M. C.

Dust spray vs. liquid.—CRANDALL[20] reports the results of a very thorough study of the comparative merits of the dust spray and the ordinary liquid Bordeaux mixture against the scab and sooty blotch of apple and the codling moth and curculio of apple. The dust spray cost about 52 per cent less than the liquid spray and there was further gain in the reduced weight of material to be transported about in the orchard. On the contrary there seemed to be no difference in the thoroughness of application under similar conditions, and the workmen were unanimous in considering the liquid spray the least disagreeable one to apply. And then as to the final and most important test, that of efficiency, CRANDALL says, in conclusion, "The results of the experiments are sufficiently decisive to warrant the conclusion that dust spray is absolutely ineffective as a preventive of injury from prevailing orchard fungi, and that it is considerably less efficient as an insect remedy than is the liquid method of applying arsenites." —E. MEAD WILCOX.

Nature of starch.—In a recent article, FISCHER[21] scouts the idea suggested by CZAPEK[22] that starch may be a mixture of colloidal and crystalline materials, saying that so far as he knows there is not the slightest evidence for such a belief.

[19] BENSON, MARGARET, SANDAY, ELIZABETH, and BERRIDGE, EMILY, Contributions to the embryology of the Amentiferae. Part II. *Carpinus Betula*. Trans. Linn. Soc. London Bot. II. **7**:37–44. *pl. 6.* 1906.

[20] CRANDALL, C. S., Spraying apples. Relative merits of liquid and dust applications. Bull. Ill. Exp. Stat. 106:205–242. *pl. 1–9. figs. 1–5.* 1906.

[21] FISCHER, HUGO, Ueber die colloidale Natur des Stärkekörner und ihr Verhalten gegen Farbstoffe. Beihefte Bot. Cent. **181**:409–432. 1905.

[22] CZAPEK, F., Biochemie der Pflanzen 1. Jena 1904.

He does not refer to the work of KRAEMER[23] or of MAQUENNE and ROUX,[24] who independently and from very different standpoints have found evidence of such a mixture. Since starch shows seven characteristic colloidal properties and only two crystalline properties he concludes that it is a colloid.

The author discusses at length the theories of staining with anilin colors, dismisses as wrong the adsorption theory, and concludes that, while in some cases, as in the staining of proteids, the reaction may be largely chemical, in most cases the taking up of the color is by solution, dyes not soluble in water being soluble in starch. He further concludes that the solution is a liquid and not a solid solution, the colloidal starch in the swollen grains being in a liquid state.—EDNA D. DAY.

Heterospory in Sphenophyllum.—This genus has been regarded as strictly homosporous, but THODAY[25] now describes and figures a section through the strobilus of *S. Dawsoni* which shows two adjacent sporangia, one of them containing spores of uniform size, the other containing fewer and larger spores, among which are seen numerous very small aborted ones. These contrasting sporangia certainly suggest heterospory, but the largest of the supposed megaspores has only about 1.5 times the diameter of the spores of the other sporangium. It will be remembered that in *Calamostachys Casheana* the megaspores are only three times as large as the microspores, and this was felt to be a remarkably small difference.—J. M. C.

Proteid metabolism in the ripening barley grain.—The first section of a paper to consist of three has been presented by SCHJERNING.[26] A short notice to call the attention of physiologists is appropriate here, but the reliability of the methods and conclusions must remain unconsidered. The author finds that species, variety, or type *per se* do not affect the chemical composition of the dry matter of the grain so far as the nitrogenous and mineral constituents are concerned. As the grain develops to maturity there is a constant tendency toward equilibrium between the nitrogenous constituents, which is established at maturity and which is not disturbed during subsequent storage except in the case of certain albumins.—RAYMOND H. POND.

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[23] KRAEMER, HENRY, The structure of the starch grain. BOT. GAZETTE. **34**: 341. 1902.

[24] MAQUENNE et ROUX, Sur la constitution, la saccharification et la rétrogradation des empois de fécule. Comptes Rendus Acad. Sci. Paris **140**: 1303–1308. 1905.

[25] THODAY, D., On a suggestion of heterospory in *Sphenophyllum Dawsoni*. New Phytol. **5**: 91–93. *figs. 14.* 1906.

[26] SCHJERNING, H., On the protein substances of barley, in the grain itself and during the brewing processes: First section: On the formation and transformation of protein substances during the growth, ripening, and storage of barley. Compt.-Rend. Lab. Carlsberg **6**: 229–305. 1906.

Lolium-fungus and smut.—In a short paper FREEMAN[27] points out the probability of relationship between the fungus of *Lolium temulentum* and the smuts. Partly by reason of the facts discovered by MADDOX, and later independently discovered by BREFELD and by HECKE, that the loose smut of wheat and the smut of barley can infect the young ovary directly, and that these grains, apparently normal, produce smutted plants, he is led to the belief that the Lolium-fungus is a smut. The behavior and appearance of the smut-mycelium in these embryos is very similar to that of the Lolium-fungus, and strongly suggests a relationship between that fungus and the smuts.—H. HASSELBRING.

Contributions from Gray herbarium.[28]—In the most recent contribution of this series, ROBINSON has published some results of his studies in the Eupatorieae. There is a revision of Piquieria, 19 species being recognized, 4 described as new, and a new sub-genus (*Erythradenia*) established; also a revision of Ophryosporus, 17 species being recognized. Under the genus Helogyne its synonyms are discussed, and its 4 species described (one of them is new). A fourth part of the contribution gives diagnoses and synonymy of Eupatorieae and of certain other Compositae which have been classed with them, among which appear descriptions of 6 new species of Eupatorium.—J. M. C.

N. Am. Characeae.—ROBINSON[29] has published a synopsis of the North American species of Chareae, one of the two subfamilies of Characeae. Of the four genera making up this subfamily, only Chara has been collected in North America. Within the range assigned, 50 species are described as belonging to this genus, 16 of which are characterized as new.—J. M. C.

Assimilation of free nitrogen by fungi.—From a discussion of the results of recent work relating to the assimilation of free nitrogen by fungi, HEINZE[30] comes to the conclusion that elementary nitrogen is not assimilated by fungi other than bacteria. The article is useful in that it brings together all the literature relating to this subject.—H. HASSELBRING.

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[27] FREEMAN, E. M., The affinities of the fungus of *Lolium temulentum* L. Annales Mycol. **4**: 32–34. 1906.

[28] ROBINSON, B. L., Studies in the Eupatorieae. Contributions from the Gray Herbarium of Harvard University. N. S. No. 32. Proc. Amer. Acad. **42**: 1–48. 1906.

[29] ROBINSON, C. B., The Chareae of North America. Bull. N. Y. Bot. Gard. **4**: 244–308. 1906.

[30] HEINZE, BERTHOLD, Sind Pilze imstande den elementaren Stickstoff der Luft zu verarbeiten und den Boden an Gesamtstickstoff anzureichern? Annales Mycol. **4**: 41–63. 1906.

NEWS.

THE UNIVERSITY OF VERMONT has conferred the degree of doctor of science on Mr. C. G. PRINGLE, keeper of the herbarium of the university.—SCIENCE.

DR. HENRY S. CONARD, professor-elect of biology in Randolph-Macon College, has resigned to accept an appointment as professor of botany in Iowa College, at Grinnell, to succeed Professor FINK.

PROFESSOR R. B. WYLIE, professor of biology in Morningside College, has been appointed assistant professor of botany in the University of Iowa, where he is to have especial charge of the work in plant morphology.

THE APPROPRIATION for the Department of Agriculture for the fiscal year beginning July 1, 1906, aggregates $9,932,940. Among the items of interest to botanists are the following: Bureau of Plant Industry, $1,024,740; Forest Service, $1,017,500; Agricultural Experiment Stations, $974,860; Division of Publications, $248,520; Bureau of Soils, $221,460; Biological Survey, $52,000; Library, $25,880.

FOR TWO YEARS the State Weather Service of Maryland has been carrying on a Botanical Survey of the State under the direction of Dr. FORREST SHREVE, Johns Hopkins University. During the present summer two parties are in the field: one under Dr. SHREVE, working in the Appalachian valley; and one under Mr. FREDERICK H. BLODGETT, Maryland Agricultural College, working in the Blue Ridge region.

THE OFFICE of Experiment Stations of the United States Department of Agriculture has undertaken the preparation of a complete list of the books written by agricultural college and experiment station men in the United States. As a heritage from the Paris and St. Louis expositions the Office has a set of about two hundred books by experiment station men. A list of these and of a few others by the same authors has been prepared, and assistance is requested in completing the list. The Office desires to get copies of such books as are not now in its collection, so far as this is possible.

—THE *Association internationale des botanistes* decided last year at Vienna to form an international organization to advance the interests of agriculture and horticulture by the selection, introduction, and distribution of plants useful for forests, fields, industrial supplies, or ornament. To this end a conference is to be held in Paris, August 25, at the building of the Horticultural Society, 84 rue de Grenelle, where it is expected to organize for this purpose a special section of the Association and to devise means for attaining promptly the ends in view. M. PHILIPPE L. DE VILMORIN is organizing this meeting, which gives promise of being successful, inasmuch as the cooperation of many *savants practiciens* and botanical gardens is already assured.

To replace Plate I, inverted in July number.

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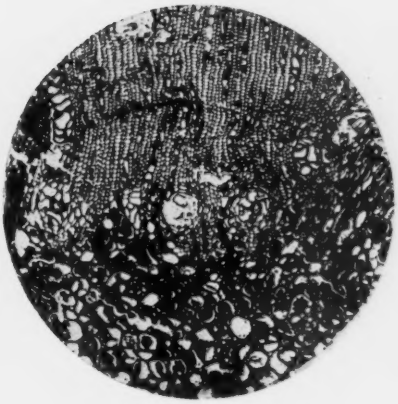

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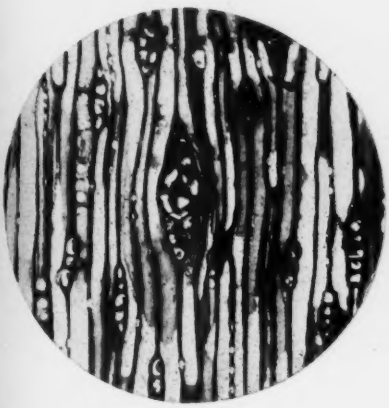

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JEFFREY & CHRYSLER on PITYOXYLA